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SHOREBIRDS, SHELLFISH(ERIES) AND SEDIMENTS AROUND GRIEND, WESTERN WADDEN SEA, 1988-1996

Theunis Piersma & Anita Koolhaas



Nederlands Instituut voor Onderzoek der Zee

The cover gives an aerial view of Griend from the west-southwest, with the northern and northeastern intertidal flats in the background (the photograph was made in early September 1996). Five Knots *Calidris canutus* are considering a landing, and a shorter or longer stopover, on the intertidal flats around Griend. For them, an important consideration will be the presence or absence and availability of their favourite foods, small molluscs. Even if present, the latter try to escape the attentions of shorebirds like Knots by hiding deep in the sediment (see inset at left, showing a deep living Baltic Tellin *Macoma balthica*). Researchers wanting to evaluate the use of intertidal flats by shorebird species such as Knots must therefore not only measure densities and size distributions of potential mollusc prey in relation to sedimentary and other environmental characteristics, but also the depth of living of the burrowing species.

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SHOREBIRDS, SHELLFISH(ERIES) AND SEDIMENTS AROUND GRIEND, WESTERN WADDEN SEA, 1988-1996

Single large-scale exploitative events lead to long-term changes of the intertidal birds-benthos community

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ABSTRACT

Intertidal bivalves on which Knots, *Calidris canutus*, a trophically very specialised molluscivore, feed, are an interesting resource for humans also. Consequently, on the intertidal flats around the island of Griend in the western Dutch Wadden Sea, the stocks of adult Blue Mussels *Mytilus edulis* and Edible Cockles *Cerastoderma edule* were depleted in 1988-1990 during intense bouts of fishery.

This report documents the year-to-year changes in the abundance of molluscs and the occurrence and diet of Knots near Griend over a nine-year period (1988-1996). Mechanical fisheries for *Mytilus* and *Cerastoderma* not only removes biomass, but has consequences for the structure of the benthic environment due to extensive sediment reworking (industrial cockle dredging), a large reduction in the production of silty (pseudo-)faeces with sediment binding properties (disappearance of mussels and cockles), an increase of tidal prism and a decrease of the lee from storms (disappearance of mussel banks), so we also investigated changes in sediment characteristics. The research was curiosity-driven and based at the Zoological Laboratory of the University of Groningen and the Netherlands Institute for Sea Research (NIOZ) at Texel; this particular study is a serendipitous by-product.

The numbers of Knots staging at the intertidal flats around Griend showed dramatic declines from 1988 to 1992 in concert with an increase in the coarseness of the sediments and serious declines in the stocks of their preferred food, the Baltic Tellin *Macoma balthica*. From 1993 to 1996 the numbers of Knots using the Griend flats were somewhat higher again due to two

summers with good spatfall of an alternative prey, the Soft-shell Clam *Mya arenaria*. In spite of this amelioration of the food situation for Knots, by 1996 *Cerastoderma* and *Macoma* had still not returned in densities comparable to the pre-fishing era, as documented in 1988. The permanent losses of bivalves were most pronounced in the sectors of intertidal flat that were most affected by the shellfisheries in 1988-1990. In fact, in these sectors Knots have yet to return in any numbers. The absence of a recovery of mollusc stocks sharply contrasts with the well-documented situation in a nearby part of the Wadden Sea, Balgzand, which is much less exposed to winds and tides. In this area both *Cerastoderma* and *Macoma* have rebounded after the overfishing of 1988-1990. However, even at Balgzand, the more exposed parts with coarser sediments were more permanently affected than the less-exposed and siltier parts found in the lee of the dykes.

We suggest that, depending on the geographic position of intertidal flats in terms of exposure to winds and tides, modern dredging techniques and the removal of mussel banks can have very long-lasting effects on the whole intertidal ecosystem. Almost a decade after the fisheries, there are still no signs of significant recovery. It is quite possible that the removal of intertidal Blue Mussel banks in combination with the sediment reworking by cockle-dredging has changed the system permanently and on a very large scale into a more dynamic ecosystem, one in which densities and availability of buried bivalves, and hence the availability of prey for some of the high-arctic migrant shorebirds, have been permanently decreased.




SYNOPSIS

Sinds het midden van de jaren zeventig is op droogvallende wadplaten in de Nederlandse Waddenzee een grootschalige, mechanische visserij van kokkels *Cerastoderma edule* tot ontwikkeling gekomen. Rond Griend, een centraal gelegen onbewoond eilandje in de westelijke Waddenzee met belangrijke broed- en rustplaatsen voor wadvogels, werden in september 1988 de kokkels volledig weggevisst. Korte tijd later, in 1989 en 1990, werden de mosselbanken (*Mytilus edulis*) bij Griend weggehaald.

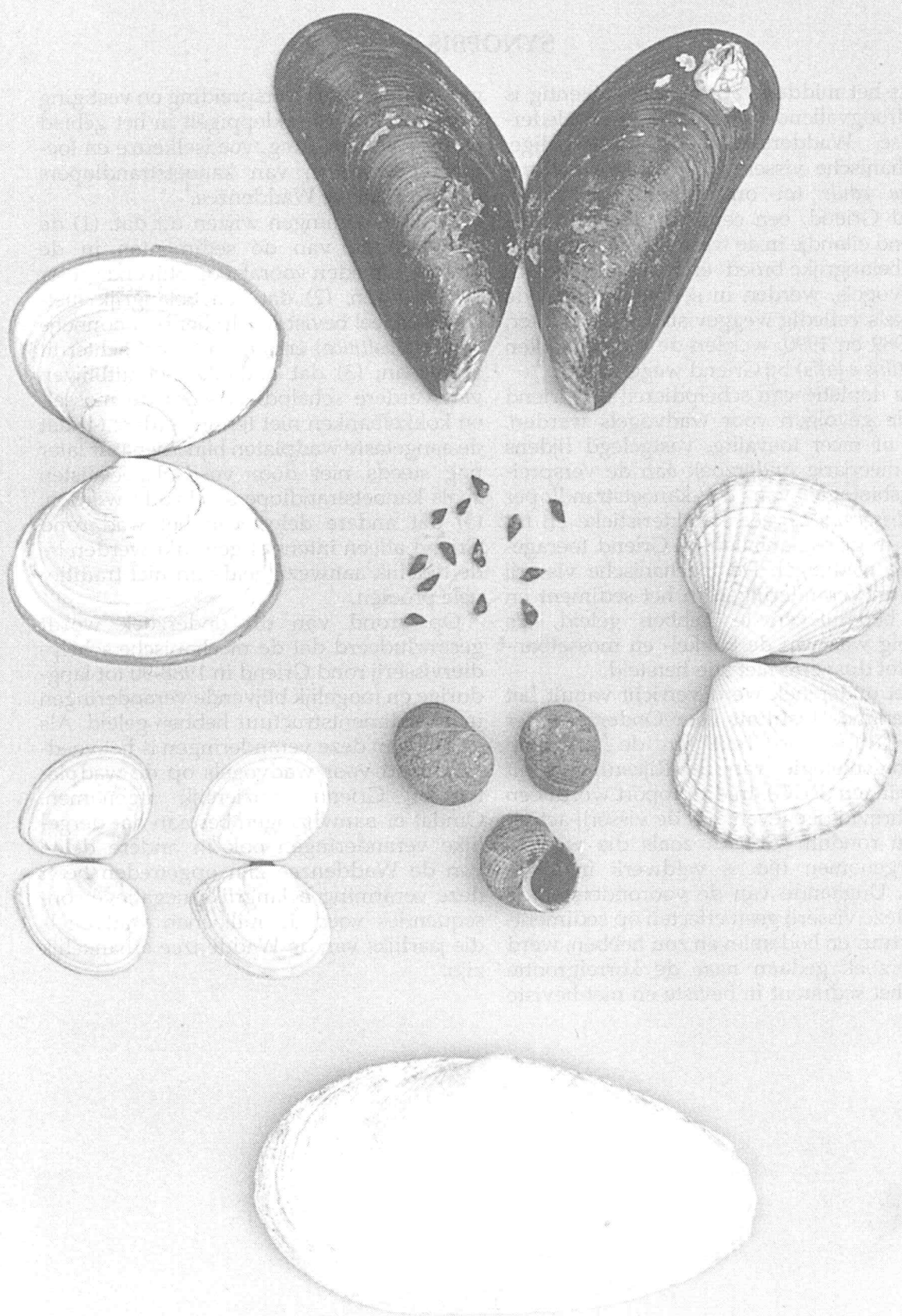
De depletie van schelpdieren op Griend en de gevolgen voor wadvogels werden, min of meer toevallig, vastgelegd tijdens een meerjarig onderzoek aan de verspreidingsbiologie van de kanoetstrandloper *Calidris canutus*, een karakteristieke en tot 1988 in grote aantallen bij Griend foeragerende wadvogel. De mechanische visserij lijkt tot veranderingen in het sediment en het bodemleven te hebben geleid, als gevolg waarvan de kokkel- en mosselbanken tot dusverre niet zijn hersteld.

Het onderzoek werd verricht vanuit het Nederlands Instituut voor Onderzoek der Zee (NIOZ) op Texel en de vakgroep Gedragsbiologie van de Rijksuniversiteit Groningen (RUG). In dit rapport wordt een beschrijving gegeven van de visserij-activiteiten rondom Griend, zoals die werden waargenomen tijdens veldwerk in 1988-1996. Uitgaande van de vooronderstelling dat deze visserij geen effecten op sedimentstructuur en bodemleven zou hebben, werd onderzoek gedaan naar de korrelgrootte van het sediment in beviste en niet-beviste

gebieden, naar de verspreiding en vestiging (zaadval) van tweekleppigen in het gebied en naar verspreiding, voedselkeuze en foerageergewoonten van kanoetstrandlopers in de Westelijke Waddenzee.

De waarnemingen wijzen uit dat: (1) de korrelgrootte van de sedimenten in de beviste gebieden vooralsnog blijvend groter is geworden; (2) dat een belangrijk niet-commercieel bevist schelpdier (het nonnetje *Macoma balthica*) ernstig in aantal achteruit is gegaan; (3) dat ondanks het uitblijven van verdere schelpdiervisserij de mossel- en kokkelbanken niet terugkeerden; (4) dat de aangetaste wadplaten bijna tien jaar later nog steeds niet door voedselspecialisten zoals kanoetstrandlopers gebruikt worden; (5) dat andere delen van het wad rond Griend alleen intensief gebruikt werden bij de tijdelijk aanwezigheid van niet-traditionele prooien.

Op grond van dit onderzoek wordt geconcludeerd dat de mechanische schelpdiervisserij rond Griend in 1988-90 tot langdurige en mogelijk blijvende veranderingen in de sedimentstructuur hebben geleid. Als gevolg van deze veranderingen is het voedselaanbod voor wadvogels op de wadplaten bij Griend aanzienlijk afgenomen. Omdat er aanwijzingen bestaan dat dergelijke veranderingen ook in andere delen van de Waddenzee zijn opgetreden heeft deze verarming belangrijke negatieve consequenties voor de miljoenen wadvogels die jaarlijks van de Waddenzee afhankelijk zijn.



SAMENVATTING

Het Nederlandse Waddengebied en haar natuurlijke rijkdommen zijn veel besproken, veel geroemd, en ogenschijnlijk beschermd door een groot aantal wettelijke maatregelen. Niettemin neemt het gebruik van de natuur in het Waddengebied voortdurend toe. In de Waddenzee zijn de visserij-activiteiten de laatste 25 jaar sterk uitgebreid. De mossel-industrie heeft zich in het begin van de zestiger jaren in de westelijke Waddenzee gevestigd, en de kokkelvisserij maakte in de tachtiger jaren een periode van sterke mechanisering door, waardoor de oogst aanmerkelijk toenam.

Op en rond Griend werd in augustus 1988 een begin gemaakt met een langjarig onderzoek aan de verspreidingsbiologie van een karakteristieke wadvogel, de kanoet (-strandloper) *Calidris canutus*. Dit onderzoek werd verricht vanuit het Nederlands Instituut voor Onderzoek der Zee (NIOZ) op Texel en de Vakgroep Gedragsbiologie van de Rijksuniversiteit Groningen. Tijdens dit onderzoek werden er gedetailleerde metingen verricht aan de aantallen, de verspreiding, de grootte- en diepte-verdelingen van de prooidieren van deze steltlopers (met name ingegraven tweekleppige schelpdieren en de aan het wadoppervlak levende wadslakjes), en werden ook het dieet, de aantallen en de verspreiding van de kanoetstrandlopers in kaart gebracht. Om de sedimentaire gesteldheid van de foerageergebieden van de kanoeten goed te kunnen karakteriseren, werd aan het begin van het onderzoek een groot aantal bodemmonsters genomen.

Eind september 1988 werden de rijke kokkelbanken op het wad ten noorden van het eiland Griend mechanisch geoogst door zes vissersschepen. Door springtij en opstuwning van het water door een zware westers storm konden de kokkels ook vlakbij het eiland worden geoogst. Na afloop van de visserij was het op het noordwad een ravage. Er lagen veel levende en halfdode nonnetjes aan het wadoppervlak, overal lie-

pen diepe ploeg- of zuig-sporen, en op veel plaatsen was de diepe dode-schelpplaag naar boven gewerkt. Net voor de visserij hadden wij onze bodembemonstering gereed, en dat was maar goed ook. Tot en met het daarop volgende najaar was het onmogelijk om 'fatsoenlijk' bodemmonsters te nemen en te zeven; het steken en sorteren van de monsters werd ernstig bemoeilijkt door de grote hoeveelheid schelpresten. In de najaars- en winterseizoenen van 1989/90 en 1990/91 werden de oude mosselbanken ten noordwesten, ten zuidwesten en ten zuiden van Griend weggevist, zoals dat ook elders in de Waddenzee gebeurde. Bij Griend was er dus sprake van twee incidentele maar grootschalige visserij-incidenten die beide hun sporen kunnen hebben achtergelaten op het wad van de Grienderwaard.

In dit rapport zetten we onze onderzoeksresultaten m.b.t. sediment-karakteristieken (slibgehalte, korrelgrootte), verspreiding en dichtheid van de bodemfauna en de aantallen kanoeten en hun dieet op een rijtje, om de veel gehoorde veronderstelling te toetsen dat mechanische schelpdiervisserij-activiteiten zoals we die bij Griend waarnamen *geen* invloed hebben op de natuurwaarden van de Waddenzee.

Visserij-activiteiten werken sediment-vergroving in de hand

Uit de metingen aan korrelgrootte en slibgehalte van het sediment in 1988, in vergelijking met herhaalde meetseries in 1992, 1994 en 1996, bleek dat tussen 1988 en 1992 het sediment duidelijk grover was geworden en het slibgehalte was afgenomen. Hoewel de veranderingen tussen 1988 en 1992 het grootst waren, zette de vergroving ten westen en ten noorden van het eiland Griend zich ten minste tot 1994 door. Ten zuiden van Griend, in de luwte van de nieuwe zanddijk die in 1988 was aangelegd

om het eiland te beschermen tegen wegspoelen, was er eerst sprake van een vergroving, maar nam de mediane korrelgrootte na 1992 weer af tot het niveau van 1988. Vlakbij en op het eiland veranderden de sediment-karakteristieken het minst, hetgeen aantoont dat de korrelgrootte veranderingen niks te maken hebben met het opspuiten van de dijk bij Griend in 1988. De vergroving van de sedimenten was het sterkst in de sectoren rond Griend waar de visserij plaatsvond (de westelijke en noordelijke sectoren). Naast visserij-activiteiten zouden ook zware winterstormen aan de vergroving kunnen hebben bijgedragen. Het blijkt echter dat er in de zeven 'beschikbare' winterseizoenen na 1988 geen sprake is van grotere gemiddelde windsnelheden dan in de zeven seizoenen ervoor. Gedurende deze vijftien jaren is het aantal stormdagen kleiner dan in de jaren zestig, toen mossel- en kokkelbanken véél algemener waren dan de laatste paar jaar.

Wij concluderen dat de visserij-activiteiten op een aantal manieren de sediment-vergroving in de hand hebben gewerkt: (1) door het omploegen van de bodem tijdens zware storm zijn veel lichte sedimenten weggestroomd (dat gebeurt zelfs bij het niet-mechanisch 'handkokkelen', zie Fig. 4); (2) met het weghalen van de mosselbanken die het westelijke wad van Griend 'omarmden,' is ook de luwte die zij gaven verloren gegaan en is tevens de rand van de platen lager geworden waardoor de stroomsnelheden er hoger zijn geworden en waardoor minder slib wordt vastgehouden; (3) met het verdwijnen van de grote aantallen kokkels en mosselen is ook hun filtreercapaciteit en de productie van (pseudo-)faeces partikels verdwenen. Het zijn deze partikels die een belangrijke aanslibbende werking hebben.

Al deze mechanismen worden visueel samengevat in het 'negatieve-biodepositie-spiraal'-model, waarin aangegeven wordt dat een redelijk slibrijk sedimentair systeem uit zijn evenwicht kan raken door omploe-

ging, het wegvallen van verticale structuren zoals mosselbanken en/of door het verdwijnen van slibproducenten (Fig. 17). In deze gedachtengang kan één forse duw door een mechanische oogst verantwoordelijk zijn voor een kettingreactie waarbij een initiële sediment-vergroving leidt tot het verlies van schelpdieren die niet langer slib produceren en/of vasthouden waardoor er zich nog minder schelpdieren vestigen die geen dekking meer bieden en (pseudo-)faeces produceren, enzovoorts. Het eindresultaat van deze causale keten is een kale, zandige en voedselarme wadvlakte.

Rijkdom aan schelpdieren neemt af

Van 1988 tot 1993 maten we de rijkdom aan schelpdieren op de Grienderwaard, door langs een aantal raaien die zich in verschillende windrichtingen vanaf het eiland uitstrekten, om de 500 m een 20-tal bodemonsters te nemen. Vanaf 1993 veranderden we het systeem en werd op alle hoekpunten van een vast grid waarbij de lijnen 250 m van elkaar vandaan lagen, steeds één monster gestoken (en ook één om de wadslakjes te bemonsteren). Bij de raaimethode werden de hoogste delen van het wad vlakbij het eiland relatief intensief bemonsterd, en aangezien daar vaak de meeste broedval plaatsvond, liet een ijkning in 1993 zien dat de raaimethode een kleine onderschatting van de biomassa aan nonnetjes geeft ten opzichte van de grid-methode. Voor de kokkels vonden we geen verschil.

Nadat de kokkelaars in 1988 de grote aantallen adulte kokkels van het noordelijke en noordoostelijke wad hadden verwijderd, was het zo'n beetje gedaan met deze soort. Ieder jaar was er spraken van een kleine broedval, vooral ten oosten van het eiland, maar veel broed viel er nimmer. Nadat de mosselbanken in 1991 waren verdwenen, vormden zich ten zuiden van Griend (langs de Blauwe Slenk) pas in de zomer van 1994 twee kleine mosselbanken van ca. 3 ha. Ook deze mosselbanken wer-

den nu en dan bevist en waren in augustus 1995 weer verdwenen. De aantallen nonnetjes liepen overal rond het eiland langzaam achteruit, met een dieptepunt in 1992. Ook daarna keerden ze niet terug. Strandgapers ontbraken in de eerste jaren van deze studie, maar verschenen in 1994, toen er een goede broedval plaatsvond waarvan de schelpdieretende wadvogels profiteerden. In 1996 vond er voor de tweede keer een redelijke broedval plaats, opnieuw vooral ten zuiden en oosten van Griend. Het meest constante schelpdieretje rond Griend was het wadslakje, dat ieder jaar in grote dichtheden op de hoogste delen van het wad ten oosten van het eiland te vinden was. Voor ieder schelpdier gold echter dat de grootteverdeling (en dus de leeftijdsopbouw) van jaar tot jaar grote verschillen vertoonde.

Minder foeragerende kanoeten rond Griend

De aantallen kanoeten die rond Griend foerageerden, zijn vanaf 1988 sterk afgenomen, met een dieptepunt in 1992. In dat jaar waren de dichtheden schelpdieren te laag om profijtelijk te zijn voor de kanoeten. In augustus en september 1988 waren kanoetstrandlopers volop aanwezig bij Griend en foerageerden ze vooral ten noorden en ten noordoosten van het eiland. Ze aten toen vooral nonnetjes, die, zo bleek uit eerder onderzoek, hun favoriete prooi vormen omdat ze een goede vlees/schelp verhouding hebben en gemakkelijk uit het wad te halen zijn. Nadat de kokkelvisser eind september hun werk op het noordwad gedaan hadden, hebben we de kanoeten daar tot in 1996 nauwelijks meer terug gezien. Ook van het westwad is weinig gebruik meer gemaakt; het oostwad bleef de meest gebruikte sector rond het eiland. Het zuid/zuidoostwad, daar waar de schelpdierfauna zich het best heeft kunnen handhaven, werd iets meer gebruikt dan voorheen. Dat de kanoeten in de jaren na 1992 rond Griend konden terugkeren

ondanks de afwezigheid van goede nonnetjes-bestanden, heeft alles te maken met de tijdelijke aanwezigheid van alternatieve voedselbronnen. In 1994 en 1996 waren dat strandgapers.

De totale aantallen kanoeten die in het gebied tijdens opkomend, hoog en afgaand water werden gezien, variëren sterk van jaar tot jaar; over de periode 1988-1996 is er niet sprake van een duidelijke terugloop in hun aantallen, afgezien van een duidelijke 'dip' in 1992. Ondersteund door verspreidingsgegevens van voor-1988 zien we dat kanoeten, om hun kostje bij elkaar te scharen, nu veel verder moeten vliegen dan voorheen. Dat 'verder vliegen' kost meer energie en dus moeten ze meer eten.

Kanoeten hebben het, net als scholeksters, de laatste jaren in de westelijke Waddenzee waarschijnlijk moeilijker gekregen. Of deze moeilijkheden zich vertalen in afname van de populatiegrootte is niet zo gemakkelijk te zeggen, maar het is een teken aan de wand dat twee algemene schelpdier-etende lange-afstand-trekkers die in de Waddenzee opvetten, de kanoetstrandloper en de rosse grutto, de laatste 15 jaar ernstig in aantal achteruit zijn gegaan (met 40-50%!); zo blijkt uit wintertellingen in hun belangrijkste West-Afrikaanse overwinteringsgebied.

Fragiel ecosysteem van de Waddenzee moet beter beschermd

Dat het ecosysteem van de Waddenzee veel fragieler zou kunnen zijn dan het misschien op het eerste gezicht lijkt, heeft te maken met allerlei subtiele, vaak onbegrepen en vaak niet-lineaire ecologische processen. Deze niet-lineariteit maakt ook dat extrapolaties van bestaande kennis vaak zeer weinig zeggen. Zo kunnen de kansen op bevruchting van de eieren van schelpdieren (die hun zaad en eieren gewoon in het overliggende water 'storten'), ineens enorm afnemen als de broedpopulatie beneden een bepaalde dichtheid komt. De enorme

veranderingen in de verspreiding van kokkels over de platen in de Waddenzee suggereren dat er misschien een 'kunstmatige selectie' op het vestigingsmechanisme van kokkels heeft plaatsgevonden. De kokkels van de jaren 90 zijn echte 'slik-kokkels' die op de slibrijke delen van het wad dicht bij de kust leven, en door hun lokatie zeer gevoelig zijn voor bevrozing in strenge winters. Het 'negatieve-biodepositie-spiraal'-model dat in dit rapport geformuleerd is, vat een aantal niet-lineaire sedimentair-biologische processen samen die maken dat ruimtelijk kleine ingrepen grote gevolgen kunnen hebben.

Gedurende de laatste honderd jaar heeft de Waddenzee een aantal unieke en gecom-

pliceerde habitat typen, en daarmee veel soorten ongewervelde diersoorten, verloren. In veel gevallen zijn er goede aanwijzingen dat een toenemende visserij-druk daar mee te maken heeft. Ons veldwerk, en ook de bestudering van een grote hoeveelheid literatuur, maakt duidelijk dat we op geen enkele mogelijkheid kunnen volhouden dat de huidige vormen van visserij de natuurlijke processen in de Waddenzee ongestoord laten. Dit betekent, dat als we de ecologische rijkdom van de Waddenzee willen behouden, of willen laten terugkeren, we heel anders tegen schelpdiervisserij moeten aankijken dan de laatste vijftien jaar in Nederland gebruikelijk is geweest.

1. INTRODUCTION

This report documents the changes of an intertidal benthic community around a major bird roost in the Dutch Wadden Sea over a nine-year period (1988-1996). The study commenced just before two intense bouts of mechanical fishing on cockles and mussels. The data allow us to evaluate any positive or negative effects of these shellfisheries with respect to sediment characteristics, the abundance of benthic bivalves, and the occurrence of a shorebird species, the Knot (*Calidris canutus*).

Our study centered around Griend (Fig. 1), a key area for waders and waterbirds in the western Wadden Sea that has been protected as a breeding colony for terns since a long time (Brouwer *et al.* 1950, Veen 1994). It provides well-known and important waterbird roosts that are virtually disturbance-free as far as human beings are concerned (Veen & van de Kam 1988). Griend has been rescued from disappearing in the sea by large scale civil-engi-

neering works supported by major financial injections. Since 1988 Griend and its surrounding intertidal flats have been visited at regular intervals by scientists from the University of Groningen and the Netherlands Institute for Sea Research (NIOZ) for studies of the distributional ecology and energetics of a spectacular long-distance migrating wader, the Knot (Piersma 1994, Wiersma & Piersma 1994). This research was knowledge-, rather than society-driven (see Ens *et al.* 1994).

Amongst other things, the early studies documented serious declines from 1988 to 1992 in the standing stocks of small bivalves eaten by Knots, and therefore in the quality of Griend as a feeding area for these birds (Piersma *et al.* 1993a). At the time we suggested that this might have been due to the effects of the intense fisheries for Edible Cockles (*Cerastoderma edule*) and Blue Mussels (*Mytilus edulis*) in 1988-1990 (see Hellmann 1992). The arguments were popularly

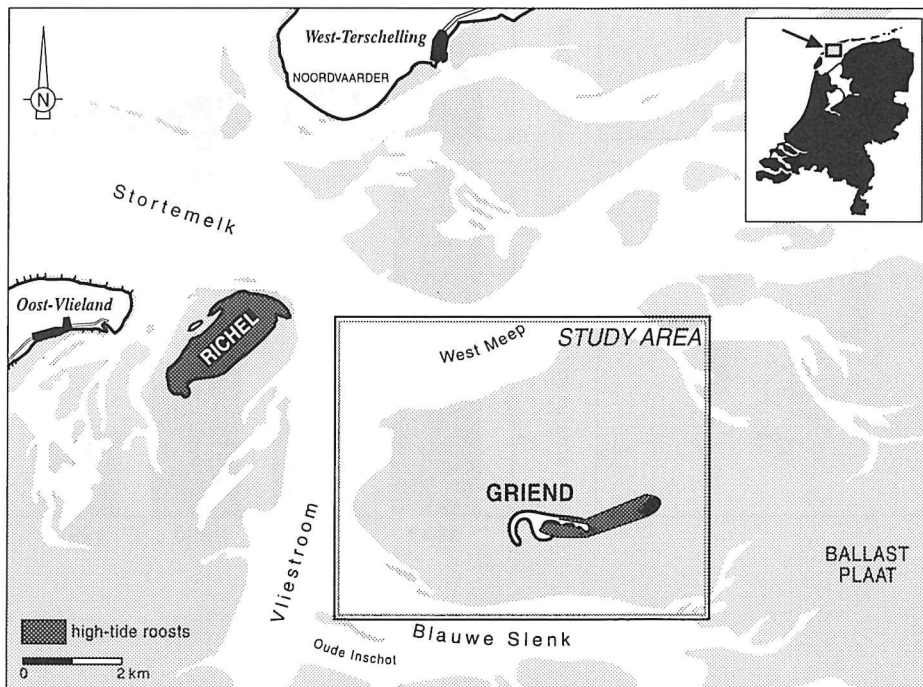


Fig. 1. Map of the position of the study area around Griend (see inset) in the western Wadden Sea of The Netherlands (see inset map of The Netherlands). Intertidal flats are indicated with a light shading, high-tide roosts of waders and waterbirds with a dark shading, and build-up areas in black.

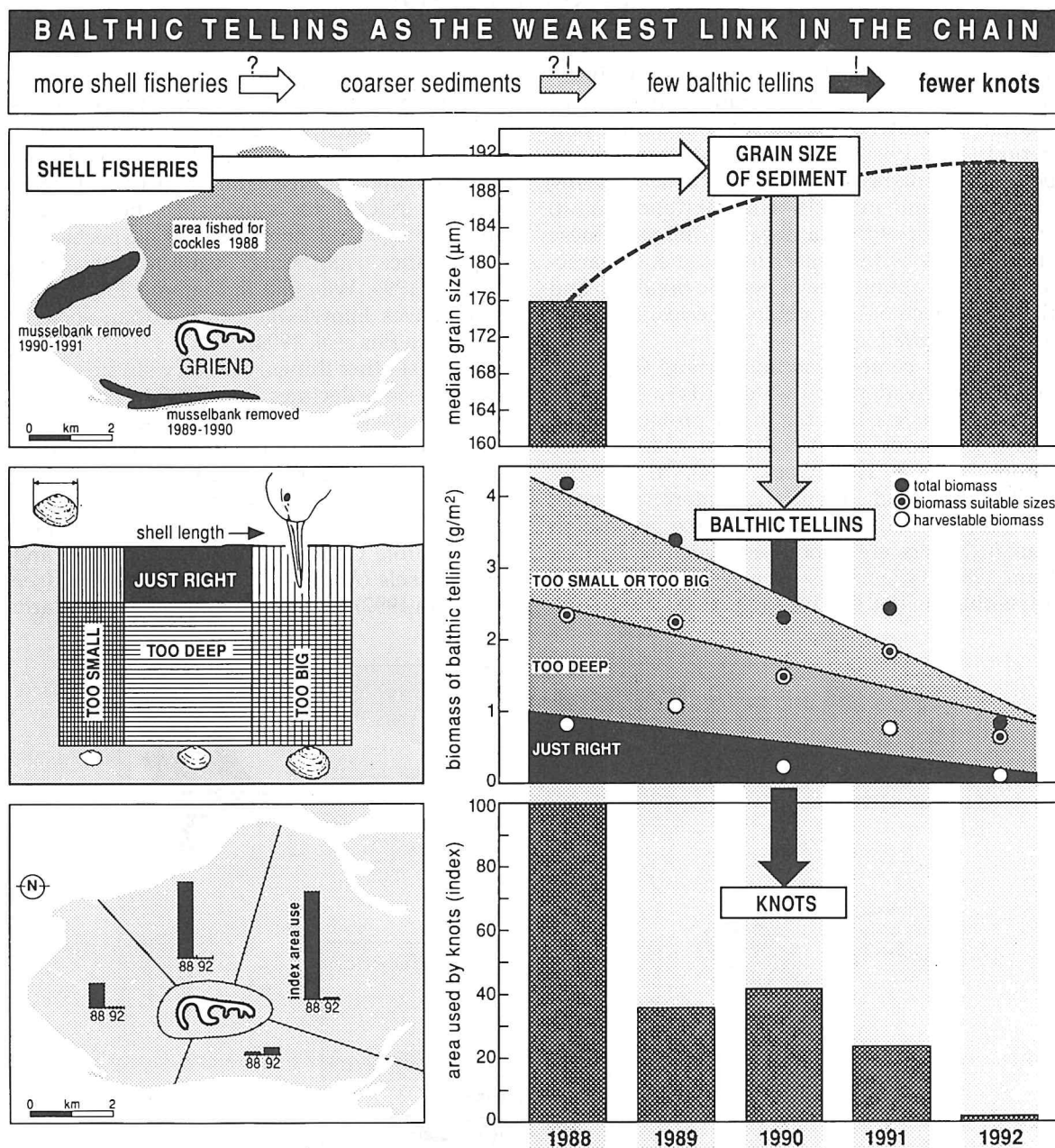


Fig. 2. A pictorial showing the approximate extents of mussel and cockle fishery around Griend (top left) in relation to changes in median grain-size (top right), the decline of stocks of Balt(h)ic Tellins *Macoma balthica* (mid right) of various categories of availability to Knots (illustrated at mid left), and a comparison of the use of the various mudflats by foraging Knots between 1988 and 1992 (lower left) and the overall changes occurring from 1988 to 1992 (lower right). A Dutch version of this scheme was published in *Waddenbulletin* in 1993 (Piersma *et al.* 1993c).

summarised in a scheme (Fig. 2) published in Dutch by Piersma *et al.* (1993c). Briefly, the actual shellfisheries and the disappearance of the protective ring of mussel banks would have lead to disturbances of the upper layer of the sediment leading to a reduced silt content and an increased grain-size of the exposed intertidal sediments around Griend. In turn, this would have reduced their value as a nursery area for shellfish brood, leading to a reduction of the standing stocks of suitable prey for molluscivores such as Knots, and henceforth to the avoidance by these birds of this formerly important area. In this report the information accumulated during a further four years of studies on sediment characteristics, standing stocks of intertidal benthic animals and the abundance and diet of Knots have been assembled. The report aims to evaluate, on the basis of nine seasons of field data for the area of intertidal flats around Griend and of comparative information and literature data from elsewhere, the interpretation made in 1993 that single incidents of intense and large-scale shellfisheries can strongly affect particular types of intertidal ecosystem with negative consequences for benthos and birds. Our null hypothesis is that the documented fishery activities have *no* such effects.

In this report we will first describe the island and its surrounding flats. The type of sediments with respect to silt content and grain-size will be dealt with in detail in view of the suggestion that sediment characteristics have changed in the course of the nine years of study. Next, the long-term changes in standing stocks of macrobenthic animals on the intertidal flats around Griend will be documented, followed by a discussion of the changes in the numbers, feeding distribution and diet of a principal avian predator, the Knot. We will then try to put the various parts into context and discuss the changes that we have seen in respect to changes in nearby intertidal flats, and in respect to possible large scale changes in the whole ecosystem of the western Wadden Sea. In the final discussion we aim to further broaden the scope and discuss the larger issues of fishery impacts. Which are the directly measurable effects of continuous shellfish harvesting in an intertidal ecosystem that is probably more fragile than we (e.g. Dankers & de Vlas 1994) have ever believed? And may there be more subtle and rather hidden effects; subtle effects that for the moment have escaped notice, but that may be relevant and become more visible in the (near) future?

2. DESCRIPTION OF THE STUDY AREA

Griend is a small uninhabited island in the western part of the Dutch Wadden Sea (53°14'N, 05°15'E; Fig. 1). What is left of Griend today are the remains of a much larger island with a permanent human settlement in the middle ages. Since then, along with many changes in the sedimentary environment of the Wadden Sea (Oost 1995a), Griend has continuously decreased in size, and would have succumbed to the waves if not for the repeated human interventions over the last century (see below, and Brouwer *et al.* 1950, Veen & van de Kam 1988, Janssen *et al.* 1994). The general public is not allowed on Griend, law being enforced during April-August by wardens/scientists living in a house on poles on the 'old island'.

The intertidal flats around Griend vary in height between -20 cm and 190 cm above D.O.L. (Dutch Ordinance Level, the 'Nieuw Amsterdams Peil', which is close to the mean-tide level). The area immediately surrounding the island, covered by our benthos and bird surveys, amounts to about 60 km². The flats are exposed for 2 to 7 hrs per low-water period. Heights, and corresponding emersion times, are greatest east and northeast of the island (Kool *et al.* 1984, Glim *et al.* 1988). The latter areas remain exposed during neap high-waters and are then used as a roosting area. West and northwest, and south and southwest, of the island, 'embracing' the western intertidal flats as it were, traditionally large mussel banks were found. These banks must have been around at least since the early 1960s (see Veen & van de Kam 1988), before being removed in 1989-1990 (see below). Also in the southeast, again at the boundary of intertidal flat and channel (Blauwe Slenk), mussel banks regularly occurred.

In the direction of Vlieland, 7.5 WNW of Griend, lies the nearest other island, Richel. Richel is a low-lying barren sand flat covering 2.4 km² that has emerged from the sea over the last 40 years. Some shorebird species (notably Knot, Grey Plover *Pluvialis squatarola* and Curlew *Numenius arquata*), feeding on the intertidal flats around Griend, often use Richel as an alternative high-tide roost, especially during spring tides.

2.1. Dike construction

From 1941 onwards, the western edge of Griend has repeatedly been enforced by various types of breakers and dikes. The last reconstruction was the largest, and was carried out before (summer 1985 when the northern beach-wall was made 500 m longer) and during the very start of this study, in August-October 1988. A 2.5-km long dike in the shape of a hockey-stick (or a banana) was built west and north of the old circular island. Griend thus increased in size from 0.16 to 0.35 km² (Essink & Bosch 1993). The central saltmarsh and creek system, often used by Knots and other shorebirds as a high-tide roost (Veen & van de Kam 1988), was left intact. Since these enforcements were made, the local topography and vegetation have changed quite a bit (Janssen *et al.* 1994). Along the short western edge of the new dike a deep gully has been formed. Parts of the dike sticking out in southward direction abraded quite quickly after 1988. The high areas with which they were replaced are now mostly covered with saltmarsh vegetation, the area of saltmarsh having encroached towards the east (Janssen *et al.* 1994). The bay between the western end of the dike and the old island has slowly filled in with sediment, and the beginnings of saltmarsh formation are now clearly established.

2.2. Fisheries

During a period of southwesterly storms that started on 23 September and lasted till 28 September 1988 (daily average wind speeds of 6-9 Beaufort on 23-24 September), suction-dredging cockle-ships appeared near Griend (an even more dramatic sight than that of the hand-cocklers in Fig. 4). During the afternoon of Monday 26 September (full moon spring tide; southwesterly stormy conditions with an average wind-force of 8 Bft), much before the predicted time of high-tide at about 22 hrs, the observers in the house on Griend were alerted by loud motor-noises of six cockle-fishing ships approaching the island to within 100-200 m of the shoreline.



Fig. 3. The visible effects of mechanical shellfisheries. (A) shows a detail of the traces left by mechanical suction-dredging cockle-ships on the intertidal flats south of Schiermonnikoog in late September- early October 1990 (photograph by Martin Poot). (B) gives an aerial view of the removal of mussel spat from an extensive intertidal mussel bank in the eastern Dutch Wadden Sea on 21 August 1991 (photograph by Piet Duiven).

The cocklers worked very close to each other over the intertidal flats north of the island, at least until darkness fell at 18.50 hr, but probably later into the night as well. The cocklers were back the next afternoon and evening, working

perhaps even closer to the island during continuing stormy weather and another spring high (27 September; predicted time of high tide ca. 22.45 hr). No cockle-ships were seen fishing on Wednesday 28 September. During the following

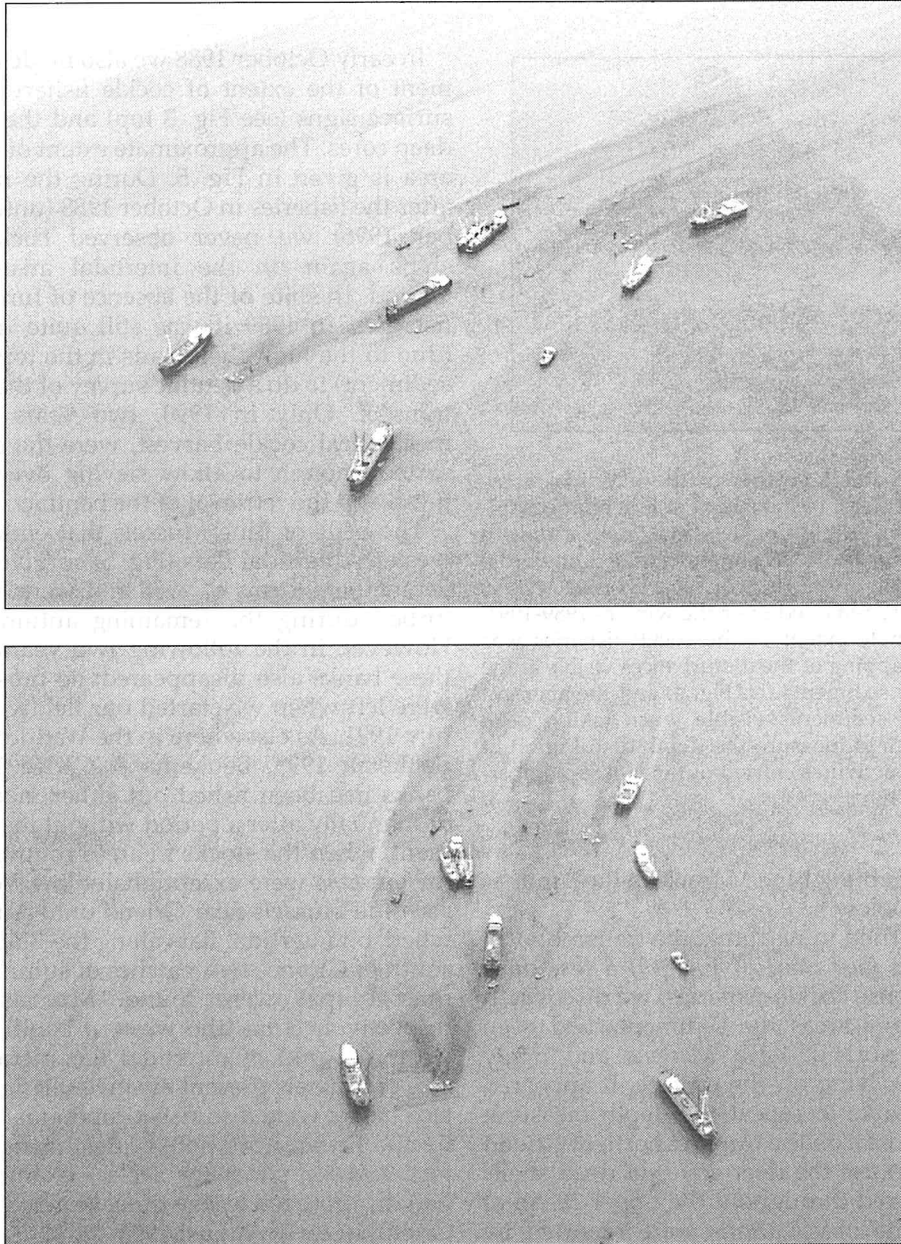


Fig. 4. Aerial views of hand-cockling in a purportedly 'subtidal' area of the western Wadden Sea close to Driesprong on 1 September 1997. The photographs were taken at 17.00 hr (summer time), when locally the tides had turned about 1.5 hrs ago. Apart from the eight mother ships and the many rubberboats and working men, the dark plumes of silt taken away from the manually reworked parts of the substrates by the incoming tides are clearly visible. (photograph by Theunis Piersma)

weeks, in situations with lower tides, cockle-fishing ships were spotted further away, north-east of the island. During a few days a week groups of cockle-ships took harbour in the

Blauwe Slenk immediately south of Griend to process (i.e. to cook and pack) the harvest and to dump the empty cockle-shells. (Incidentally, these shell deposits provided a firm settling

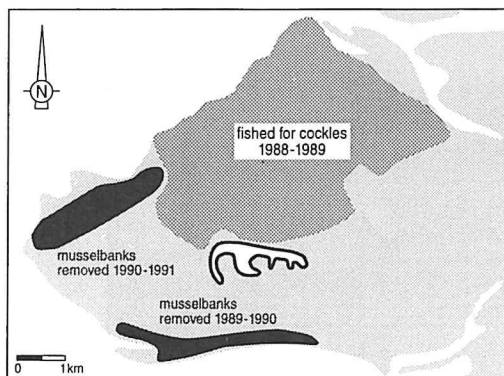


Fig. 5. Approximate extents of the intertidal areas north and northeast of the island of Griend mechanically fished for Edible Cockles *Cerastoderma edule* in the 1988 season (from 26 September 1988 onwards) and the location of the beds of Blue Mussels *Mytilus edulis* that were removed over the winters 1989-1991. The approximate extent of the cockle-fisheries was based on a mapping of the disturbances visible at the surface of the sediments (cf. Fig. 4) and the aberrant reworking of sediments visible when taking deep sediment cores to measure the depth distribution of *Macoma*, both activities carried out in late September-November 1988.

substrate for young Blue Mussels in the summer of 1994, see below.)

When we tried to resample the transect north of the island (see map of Fig. 19) a few days after the intense cockle-fisheries, we discovered that over large areas the sediments had been seriously reworked, with *Macoma* and many shell remains lying on the surface. It appeared quite impossible to repeat the depth measurements of *Macoma* on the transect north of Griend (Fig. 23), because the deep layer of dead shells had been mixed throughout the upper 20 cm of sediment. The observations were reported by car-telephone to the Ministry of Agriculture, Nature Management and Fisheries (Dr J. de Vlas) in early October 1988.

In early October 1988 we also made an assessment of the extent of cockle fishery based on surface signs (see Fig. 3 top) and the taking of deep cores. The approximate extent of the fished area is given in Fig. 5. During the nine years after the fisheries in October 1988 (until November 1996) we never observed cockle-fishing ships again on the intertidal areas around Griend. In spite of the absence of further shell-fisheries, in 1989 it was still quite impossible (due to the high shell loads in the top layers of sediment) to do a benthic survey of the northern transect. Only in 1990, two years after the mechanical cockle harvest, were the sediments sorted enough to allow sieving over a 1 mm mesh and the retrieval of the benthic animals.

The beds of Blue Mussels that embraced the western intertidal flats (Fig. 5) survived the late September storms of 1988 and were left undisturbed during the remaining autumn season. However, in the following two years much of these banks also disappeared; no mussel banks were left when we started our fieldwork in late July 1991. As elsewhere in the Wadden Sea (e.g. Beukema 1993, Beukema & Cadée 1996), the banks had been fished out either mechanically or manually after a period without mass recruitment, when the stocks in areas routinely fished for mussels were exceptionally low. We did not see Blue Mussels near Griend until August 1994 when, on intertidal flats along the Blauwe Slenk south of Griend, two patches of summer-settled mussel spat were found. Mussels covered respectively 3 ha (the western bank) and 3 ha (eastern bank) of intertidal flat (details of the size of mussels present are given in Fig. 34). The two banks were also fished upon (as evidenced by the linear scars noted later in the year; see Fig. 3 lower panel for a clear example). They had disappeared by the time we arrived back on Griend in early August 1995.

3. SEDIMENTS

The studies of Knots were set out with the ambition to explain the feeding distribution of these birds as a function of food abundance and local environmental characteristics. It had been suggested that substrate type might be important because Knots often show a preference for reasonably sandy substrates covered with a film of water (Prater 1972, Goss-Custard *et al.* 1977), and the abundance of mollusc prey is often correlated with sediment characteristics (e.g. Dankers & Beukema 1983). At the start of the study in 1988 we therefore tried to map out sediment characteristics (notably grain-size) by taking surface core samples at sites where we also sampled benthos. This exercise was repeated for the first time in 1992. Since, we have been collecting sediment samples every 1-2 years.

3.1. Methods

In early September 1988 (before the cockle fishery started), we took core samples at sites at 500 m intervals along several transects around Griend (Fig. 6 top). The locations were found by pacing out the distance with a calibrated step-length and a hand-counter, using a compass to walk the appropriate fixed bearings. In addition, two locations in the northeastern corner of the intertidal flats around Griend were sampled, their positions being reconstructed from crossreadings of compass-bearings on the 'Brandaris lighthouse' in West-Terschelling, the house on poles at Griend, and the largest church-tower of Harlingen. In 1992 the same procedures were followed, but in 1994 and 1996 (Fig. 6 two bottom panels) the sampling points were found using hand-held GPS on the basis of geographical coordinates of the 'transect-locations' read out from a map.

At each location a sediment sample was taken with a 5 cm diameter core to a depth of 7-8 cm, and the sample stored in a closed plastic bag at room-temperatures for 1-4 weeks, and at -30°C subsequently. The entire samples were first washed in fresh water, shaking the water/sediment mix, and sieved over a 50 µm mesh. The residue in the water that came through the 50 µm mesh was then collected on a pre-weighed piece of dry filter paper. After drying, the sediment and filter paper was reweighed to the

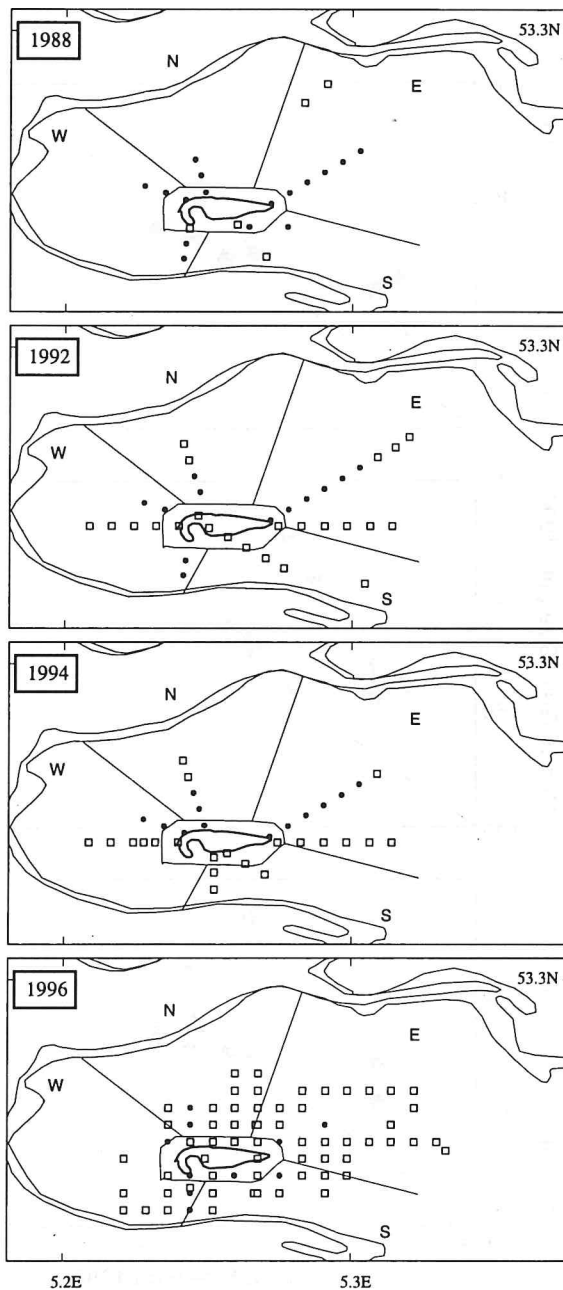


Fig. 6. Sediment sampling stations in the five sectors around Griend in 1988, 1992, 1994 and 1996. The filled dots indicate stations at which sediment samples were taken repeatedly, using 1988 as the year of reference (for the inter-year comparisons in Figs. 7 and 8). Note that the geographical coordinates of this and the other maps in this report are given in degrees, with decimal points rather than seconds after the dot.

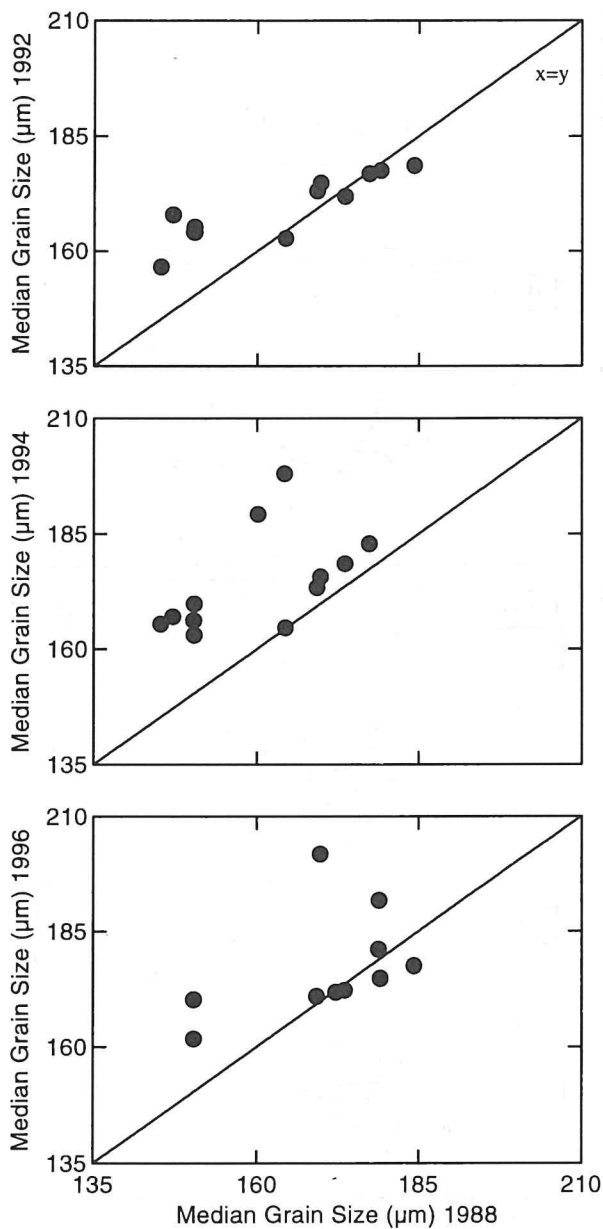


Fig. 7. Median grain-size (without silt and large particles) of the sediments at repeatedly sampled stations on the intertidal areas around Griend, using the data for 1988 (plotted on x-axis) as the yardstick for the comparisons with 1992, 1994 and 1996.

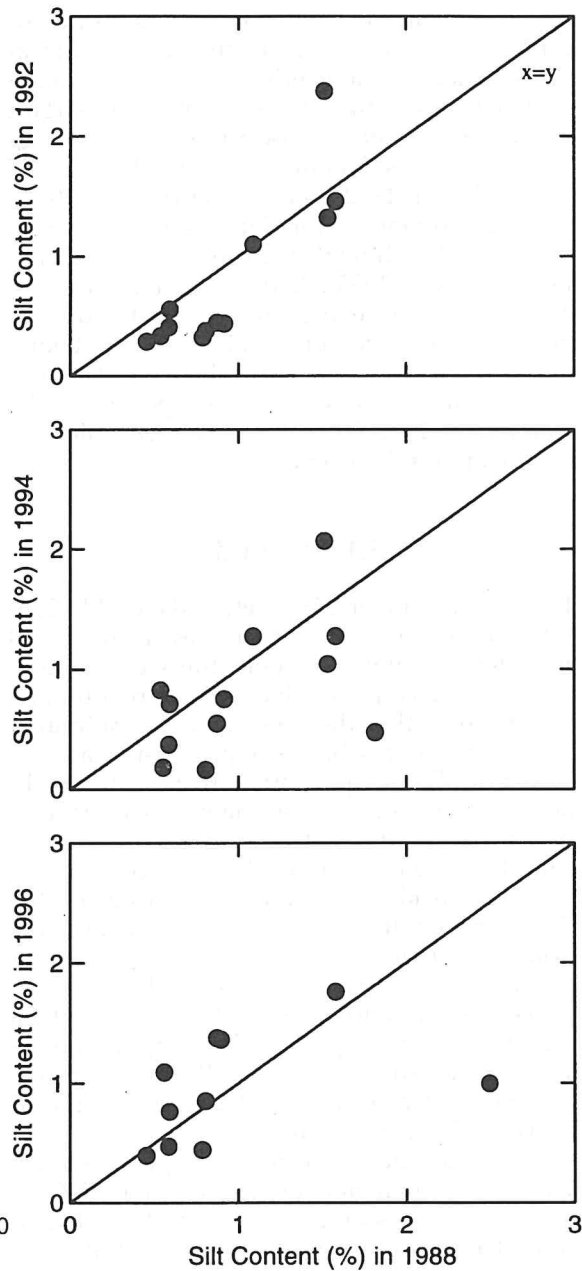


Fig. 8. Silt content (% dry mass of particles smaller than 50 μm) of the sediments at repeatedly sampled stations on the intertidal areas around Griend, using the data for 1988 (plotted on x-axis) as the yardstick for the comparisons with 1992, 1994 and 1996.

nearest mg, and the mass of the smallest grain-size fraction (everything smaller than 50 μm) obtained by subtraction. After drying the remainder of the sample to constant mass in an oven at 60°C, the sediments were sieved over sieves with meshes of 63, 125, 250, 315, 500 and 1000 μm and weighed to the nearest mg. The fractions smaller than 50 μm and larger than 1000 μm (=1 mm) were not used to calculate the median grain-size, but are presented as percentages of the total mass.

Median grain-size was computed following Krumbein & Sloss (1963: pp. 96-101) by plotting cumulative dry-mass percentage (starting with the largest grain-size fraction, i.e. those smaller than 1000 μm diameter retained on the 500 μm sieve) on the logarithm of particle diameter (according the mesh of the sieve at which the fraction was captured). From this semilogarithmic plot the median grain-size can be read off starting at the 50% cumulative dry mass on the y-axis.

Following Baretta-Bekker *et al.* (1992: p.123) we use the following terminology to describe grain-size. 'Clays' consist of particles smaller than 2 μm and were not measured separately in this study. 'Silt' refers to the fraction of particles 2-64 μm in diameter, and accordingly we have called our <50 μm fraction the silt fraction. 'Sand' refers to particles between 64 μm and 2 mm, and this category encompasses the remaining part of the sediment except for the occasional larger shell fragments. Note that the grain-size distribution is a measure of the 'energies' of the depositing medium and of the depositary basins. As a rule (in the special case of uniform volume-specific weights), coarse sediments are found in high-energy environments and finer sediments in low-energy environments.

3.2. Results

Plots of median grain-size in 1992, 1994 and 1996 against median grain-size in 1988 for locations that have been sampled repeatedly (Fig. 7), show an increase in grain-size of the surface sediments after 1988, particularly between 1988 and 1992 (when at 12 of the 12 locations median grain-size increased, Sign-test, $p < 0.0001$). This seems to be especially true for the locations that had the smallest grain-sizes to start with (calcu-

lated slopes are all smaller than unity, but only significantly different from zero at the 5% level for the 1988-1992 comparison). Consistent with this increase in median grain-size is the decrease in silt content (% dry mass of particles <50 μm) (Fig. 8), especially over the first 4 years (1988-1992, 10 of 12 locations show decreased silt contents, Sign-test, $p < 0.05$).

Box-plots of changes in median grain-size (and the changes in the percentages smallest and largest particles) over time for the different sectors around Griend, confirm the general increase in sandiness, but with interesting differences between sectors. In the western sector (Fig. 9), median grain-size increased until 1994 but then stabilised. From 1988 to 1992 the silt content of the sediment decreased, but has since increased to earlier levels. In the northern sector (the area that has perhaps endured the largest disturbances of the substrate), median grain-size increased a great deal, from 170 μm in 1988 to about 200 μm in 1992, with a stabilisation or slightly reverse trend since then (Fig. 10). Silt content was lowest in 1994, when it was only a third of that in 1988. In the eastern sector the pattern was rather similar (Fig. 11), even though the area is rather siltier and the changes in sediment characteristics not as outspoken as in the northern sector. Largest median grain-sizes were reached in 1994, at a time when silt content was also smallest. The southern sector shows a somewhat different trend (Fig. 12). Between 1988 and 1992 median grain-size increased, but since then there is a gradual decrease that continues into 1996 when median grain-sizes are lower than in 1988, and silt content higher. In the high parts of the intertidal flats immediately around the island the patterns are quite similar (Fig. 13), but with the largest median grain-size values and the smallest silt content in 1994 rather than 1992. In all sectors the percentage large particles was highest in 1994 (or 1992). An analysis of variance, taking into account statistical interactions with area of origin (sector), showed that the variation in median grain-size values between years is indeed larger than the variation within years ($F_{3,121}=8.3$, $p < 0.0001$).

A summary of the differences between the sediment characteristics around the island of Griend with respect to location and time is presented in the four panels of Fig. 14. Over these four sectors, overall average median grain-size

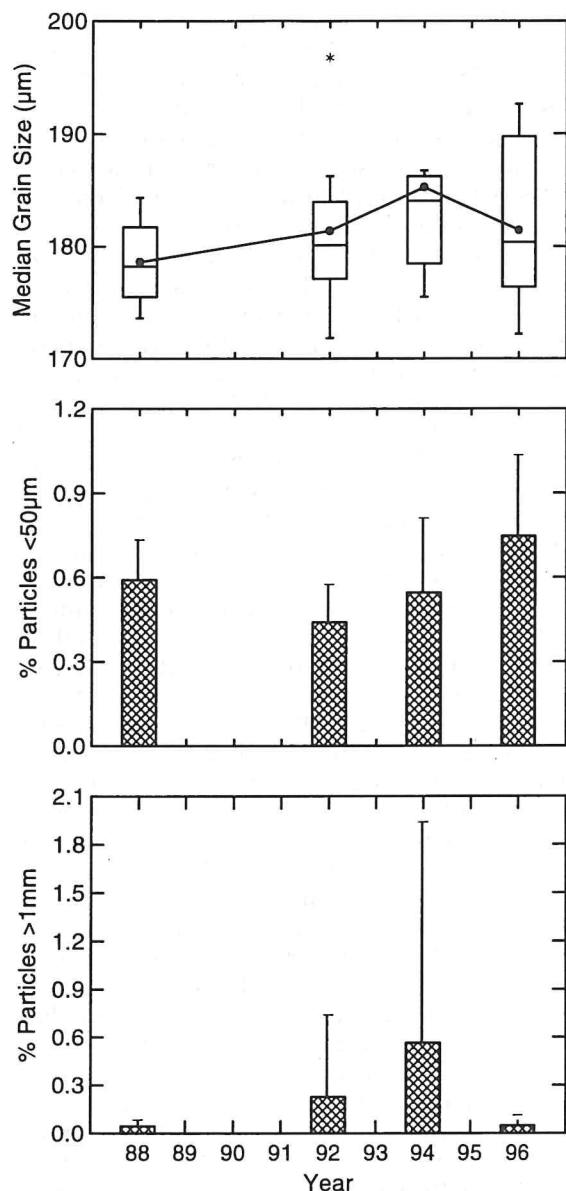


Fig. 9. Long-term changes in median grain-size (top), silt content (middle) and fraction large particles (particles retained on a 1 mm sieve; bottom) of the **western** sector of the intertidal area around Griend. Median grain-size data are given as a 'box-plot', in which the box gives the median plus or minus 25% of the values. The vertical line covers the entire distribution except outliers given by an asterisk. Averages are given as dots. The average relative contributions of small and large particles are given as histograms with one SD (vertical lines). n -values for 1988, 1992, 1994 and 1996 are respectively 4, 8, 7 and 10.

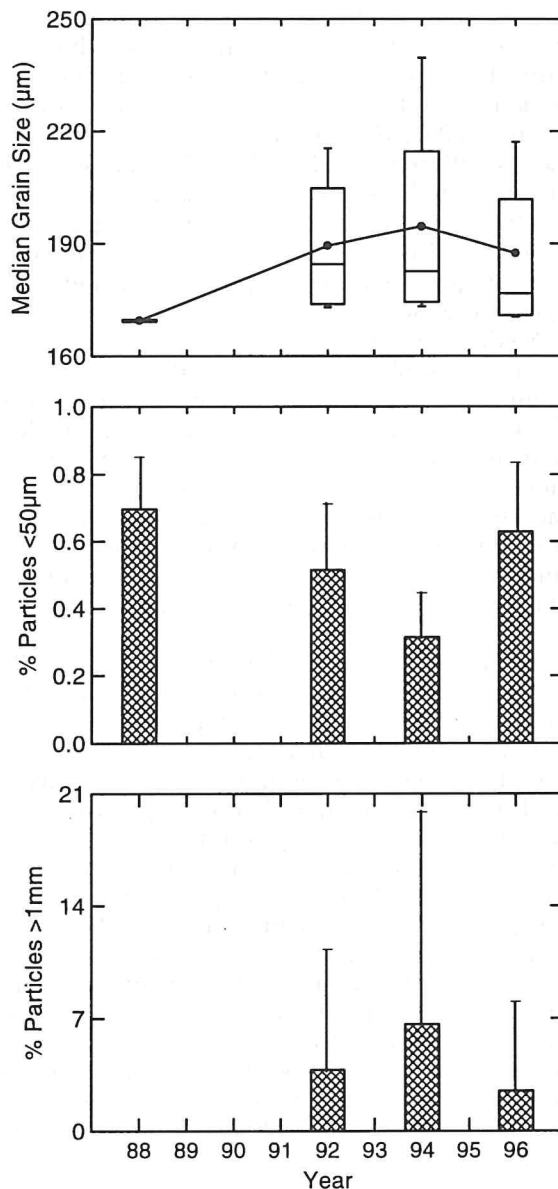


Fig. 10. Long-term changes in median grain-size (top), silt content (middle) and fraction large particles (particles retained on a 1 mm sieve; bottom) of the **northern** sector of the intertidal area around Griend. Typographical conventions as in Fig. 9. n -values for 1988, 1992, 1994 and 1996 are respectively 2, 4, 4 and 5. Note that, in view of the large spatial variation in grain-size characteristics within this sector relative to the placing of the 1988-transect (Figs. 5 and 14), for 1996 the parts of the grid were used that geographically correspond best with the earlier transect.

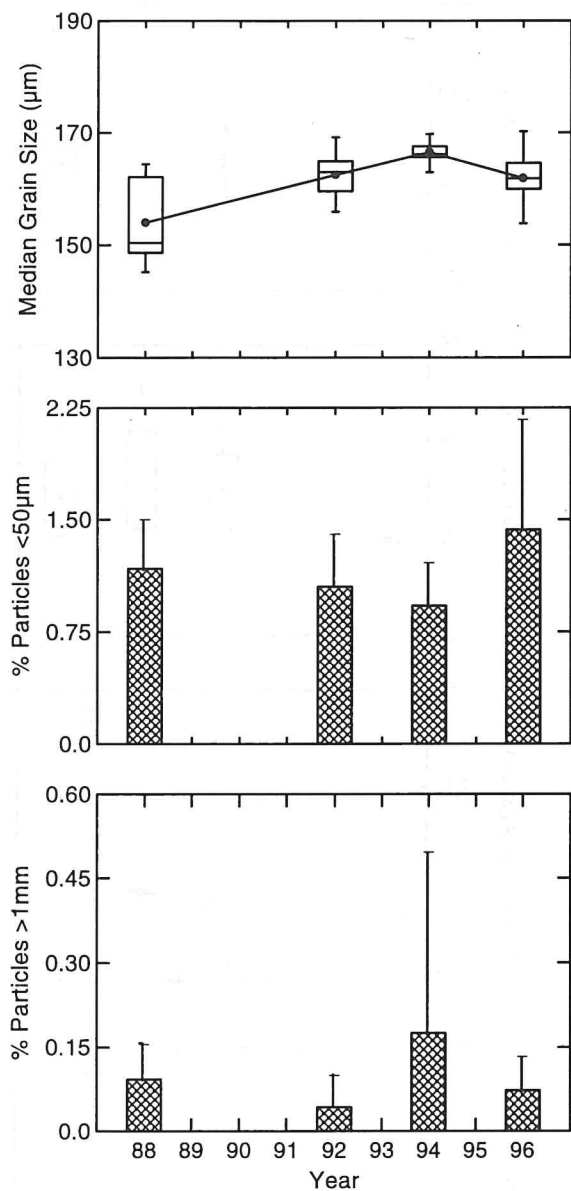


Fig. 11. Long-term changes in median grain-size (top), silt content (middle) and fraction large particles (particles retained on a 1 mm sieve; bottom) of the **eastern** sector of the intertidal area around Griend. Typographical conventions as in Fig. 9. *n*-values for 1988, 1992, 1994 and 1996 are respectively 8, 14, 11 and 26.

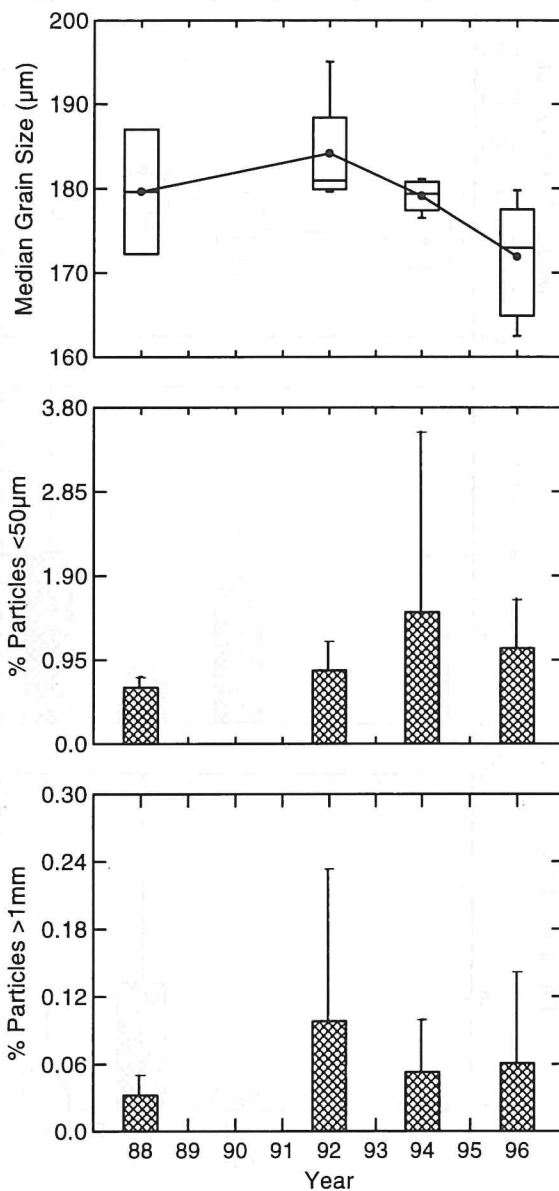


Fig. 12. Long-term changes in median grain-size (top), silt content (middle) and fraction large particles (particles retained on a 1 mm sieve; bottom) of the **southern** sector of the intertidal area around Griend. Typographical conventions as in Fig. 9. *n*-values for 1988, 1992, 1994 and 1996 are respectively 2, 4, 4 and 10.

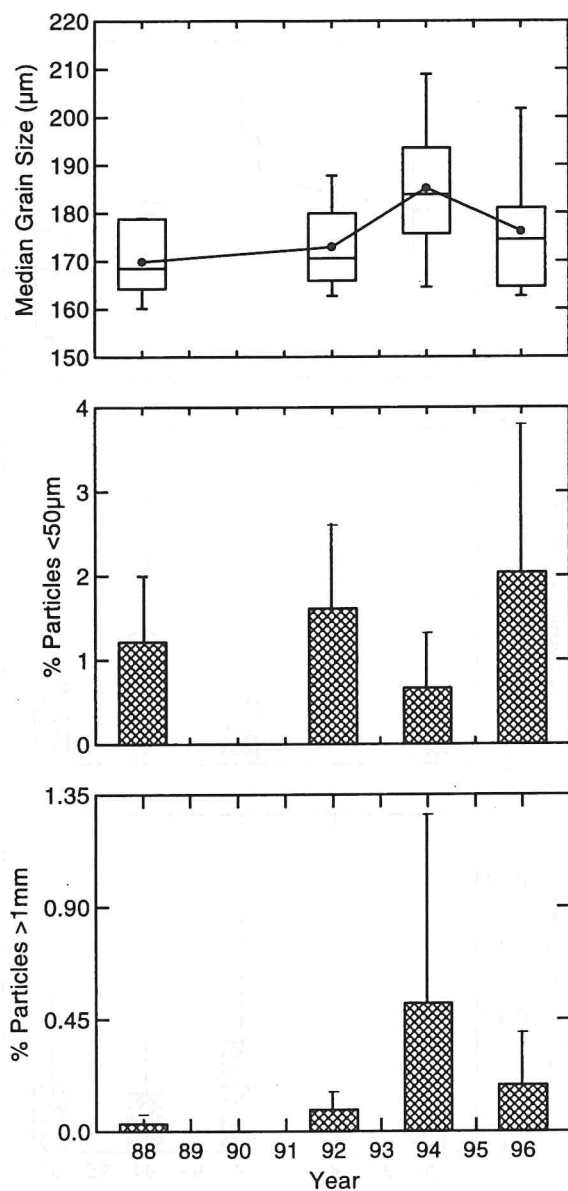


Fig. 13. Long-term changes in median grain-size (top), silt content (middle) and fraction large particles (particles retained on a 1 mm sieve; bottom) of the area immediately around (with 200 m of) the island of Griend. Typographical conventions as in Fig. 9. n -values for 1988, 1992, 1994 and 1996 are respectively 6, 4, 7 and 9.

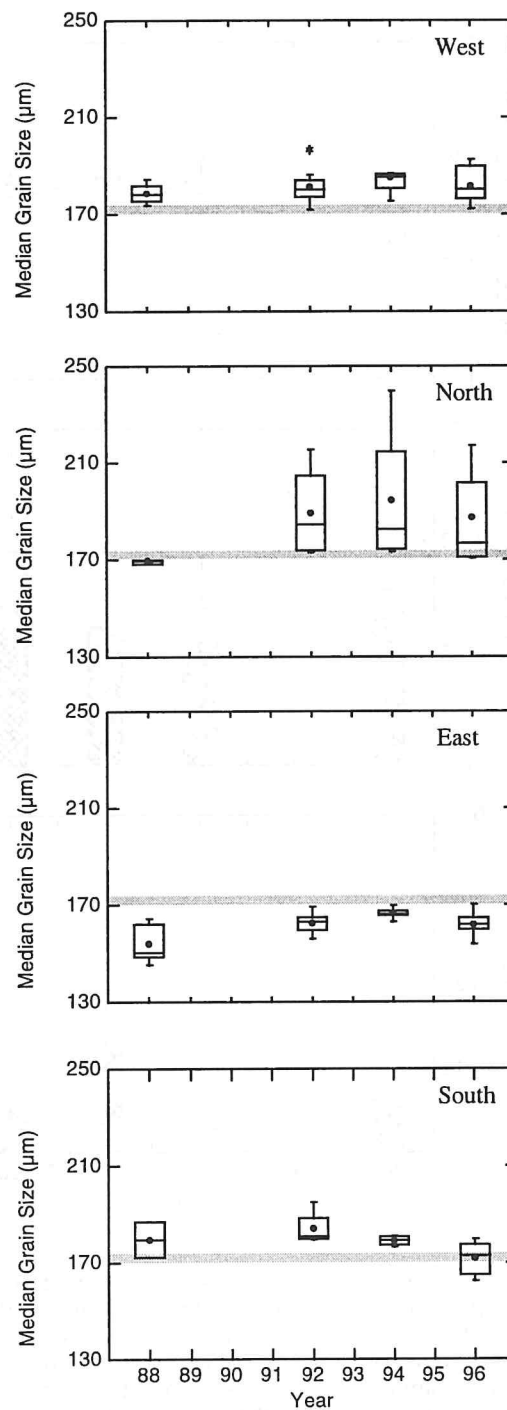


Fig. 14. Comparison of the long-term changes in median grain-size for the different sectors of intertidal area around Griend (based on Figs. 9-12). Box-plots for an y-axis with a common scale are presented in comparison with the grand mean (shaded horizontal bar) for overall median grain-size, computed over all available median grain-size values presented in this graph. Typographical conventions as in Fig. 9.

between 1988 and 1992 increased from $165.3 \mu\text{m}$ ($\text{SD}=13.5$, $n=16$) to $174.0 \mu\text{m}$ ($\text{SD}=13.9$, $n=30$). This difference is statistically significant (pooled-variance model Student's t -test, $t = -2.04$, $\text{df}=44$, $p=0.047$). However, as noticed before, there are also differences between the sectors. Indeed, a two-way analysis of variance showed a statistically significant difference between 1988 and 1992 ($F_1=9.211$, $p=0.004$) but with a very important effect of 'sector' ($F_3=25.621$, $p<0.0001$) (there were no significant interactions between the two factors). In more

general terms, although the sandiest sediments were originally found in the western and southern sectors, at least since 1992 they are found in the northern sector. The eastern sector has the finest sediments and showed the smallest changes in median grain-size. The southern sector, with intermediate median grain-size values, since 1994 shows a trend of becoming siltier.

With sediment samples collected in a grid-like fashion in 1996, it is possible for this particular year to give summary maps of median grain-size (Fig. 15 top) and silt content (Fig. 15

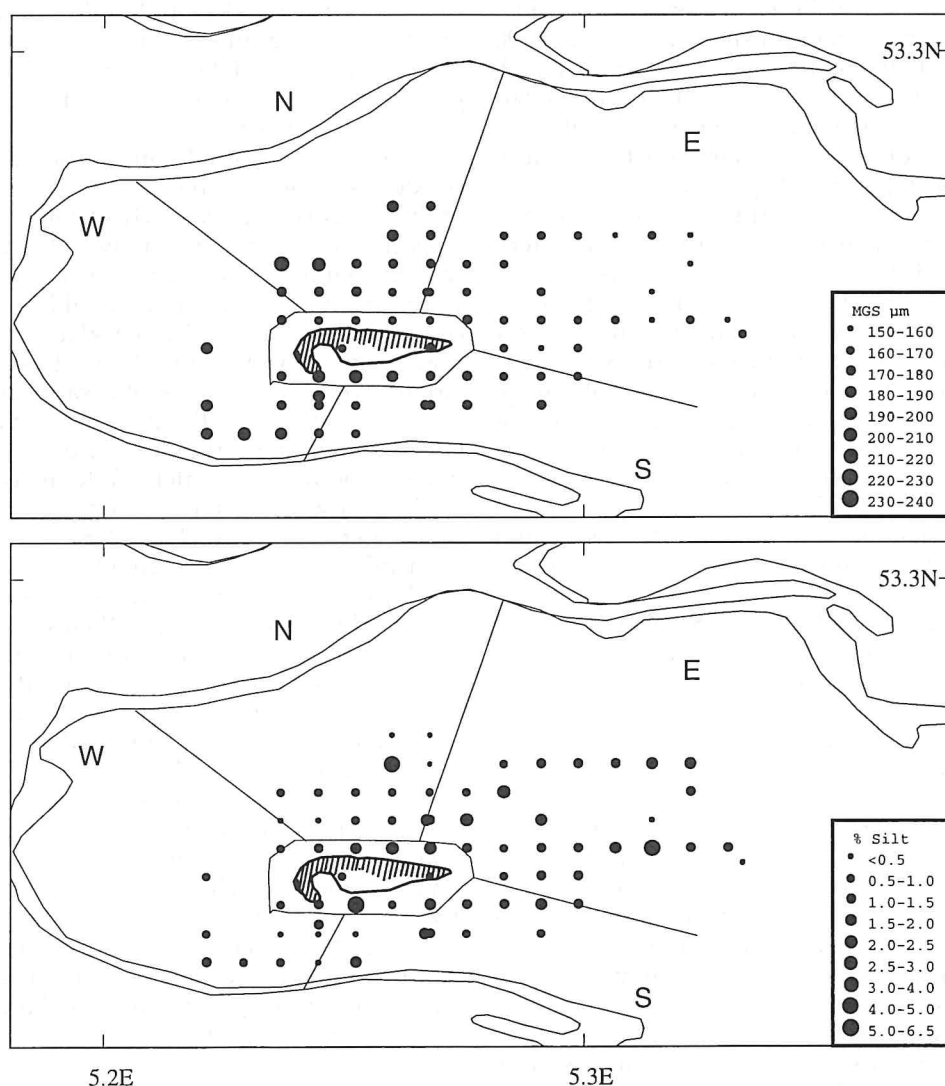


Fig. 15. Map of the spatial variations in median grain-size (top) and silt content (bottom) in 1996 for the intertidal flats around Griend. The banana-shaped enforcement to the island of Griend (built in 1987-1988) is indicated by hatching.

bottom). The maps confirm that the sandiest sediments are found in the west and north, but also immediately south of the island. The silty sediments occur rather patchily in the north and east, but a silty patch was also hit at one point just south of the island of Griend.

3.3. Discussion

With a silt content that is always less than 1.5%, the intertidal flats around Griend can, as has been noticed several times before (e.g. Piersma *et al.* 1993a), safely be characterised as sandy. The typical median grain-size values of 150-200 μm belong to the highest reported for the Dutch part of the Wadden Sea of the 1970s and 1980s (see Dankers & Beukema 1983, Zwarts 1988). A comparison of sediment characteristics in early September 1988 and August 1992 (Figs. 9-12, Fig. 14), shows that the silt fraction had decreased in the western, northern and eastern sectors and that the median grain-size had increased everywhere. Thus, large parts of the intertidal flats around Griend became coarser grained, i.e. more sandy. From the sediments collected in 1994 and 1996 it is clear that, except for the southern sector (Fig. 12), this change to coarser sediments has shown reversals only after almost a decade, and only after a relatively storm-free year (1995).

Factors that, on their own or together, could have affected sediment characteristics around Griend are: (1) the building, using the rather coarse sands from the Blauwe Slenk, of the large banana-shaped dike along the northern edge of Griend in 1987 and 1988 (see Fig. 15); (2) the respective fisheries activities around Griend in 1988-1991 (mechanical cockle fishing, including some dramatic reworking and potential loss of sediments during a period of storms, of the northern and part of the eastern sectors in late 1988, and the removal of the mussel banks from the western and southern sectors in the following two years); and (3) variations in the incidence of storms and storm surges in the area (perhaps in interaction with a small moon cycle effect, Oost *et al.* 1993).

With respect to the 'storm-factor', an analysis of the occurrence of minor and major storms (Fig. 16 top and bottom, respectively), shows that there are no differences between the incidence of storms in the seven years before 1988

compared to the seven years after 1988 (Student's *t*-tests, with *t*-values of -0.32 and -0.37 and *p*-values of 0.75 and 0.72, respectively). Indeed, the incidence of storms throughout this period seems to be rather lower than in the 1960s. With respect to the first factor (the building of Griend's enforcements), it could have been predicted that the dike (with sediment characteristics that were not very different from those of the surrounding flats), that acts as a barrier against wind and wave action, would easily have led to the build-up of silty sediments in the lee of the island. This did not happen between 1988 and 1992, but in the southern sector the median grain-size has shown a decrease between 1992 and 1996. This sector may indeed get most of the sheltering effect from storms from the northwest.

When we reported our observations on cockle-dredging and their effects to Dr J. de Vlas of the Ministry of LNV (early October 1988), the response was rather dismissive. It was argued that the kind of sediment reworking that we were observing could not possibly have been caused by the mechanical cocklers (cf. de Vlas 1982), and that the intertidal flats north of Griend were in a process of disappearing anyhow. As to the latter, the map in Eisma & Wolff (1983) shows the Grienderwaard to belong to parts of the western Dutch Wadden Sea that are eroding slowly, but more recent information of Rijkswaterstaat (Glim *et al.* 1988), indicates that from 1977-1983 the area actually was in a stable condition, with some patches even showing light deposition. Nevertheless, median grain-sizes on the Grienderwaard seem to show an increase since the 1950s (Postma 1957). As to the former dismissal, we would argue now that the obvious fishing frenzy that took place on very rich cockle-banks (see Figs. 27-30) during the storm spring tides of 26 and 27 September must have meant that the suction-dredges covered the same patches of sand flat perhaps several times in. This is because these ships always have difficulty to steer the relatively small dredges over a new course and rely on multiple crossings of small areas instead (fishing efficiency is judged on the basis of the amounts of cockles that are sucked in per unit time).

That intensive mechanical suction-dredging for cockles during the stormy and particularly high-water conditions present at the time could

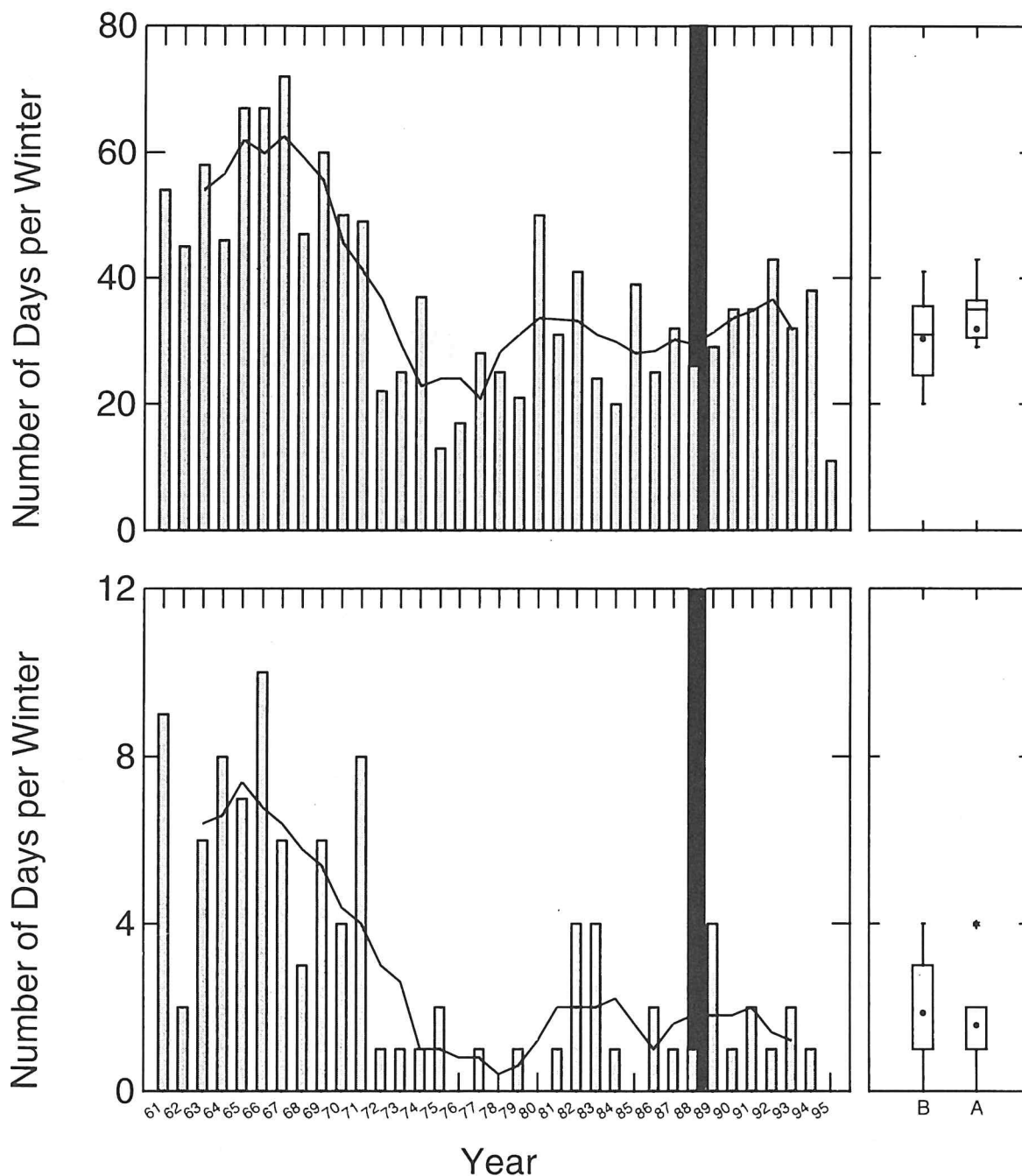


Fig. 16. Changes in the occurrence of fair winds (top panels; days with average wind speeds of 10-15 m/s, i.e. 6-7 Beaufort, calculated by us on the basis of hourly means) and storms (lower panel; days with average wind speeds of more than 15 m/s, i.e. >7.5 Beaufort) in the winter seasons of 1961-1962 (indicated by 61) to 1995-1996 (August through April), based on the published daily weather records of KNMI meteorological station De Kooi near Den Helder. To lead the eye a five-year running average was calculated (thick line). The vertical black bar indicates 1988, the year of the cockle-fishery around Griend. The box-plots on the right indicate the average numbers of days of either category in the seven years before ('B') and the seven years after ('A') the critical cockle-season, 1988-1989, with dots indicating the averages. See text for statistics.

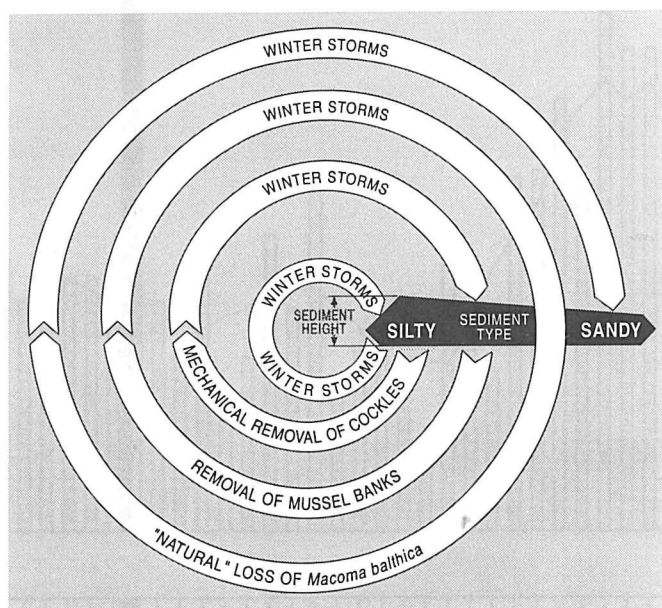


Fig. 17. Graphical model of the 'negative biodepository spiral' by which mollusc-rich and reasonably silty sediments in the lee of a mussel bank, through the successive losses of cockles due to mechanical harvesting and the mussel bank itself, transform into permanently sandy, highly dynamic and lower lying intertidal flats where even *Macoma* is unable to maintain its population (processes as they appear to have taken place near Griend in 1988-1994). Note that in the absence of human activities, the winter storms do not effect the balance of the sediments: the changes have to be kicked off by the (mechanical) removal of the stocks of large filter-feeding and faecal pellets producing bivalves (Blue Mussels and/or Edible Cockles) but can then turn into a self-perpetuating process with the additional loss of small filter-feeders.

easily have left deep scars, and could have caused the immediate loss of considerable amounts of light sediment particles in the fished areas, is illustrated by the sediment-plume generated by *manual* cocklers in shallow water with an incoming tide (Fig. 4). These photographs were taken during very calm weather and show a case of relatively modest sediment reworking. Even so, the visible effects and potential loss of silt are quite dramatic.

The shellfisheries-factor is the only correlate that can satisfactorily explain both the changes in sediment characteristics over time and the differences between the various geographical sectors around the island. The increases in median grain-size in the northern sector (Fig. 10) occurred after heavy sediment reworking (witnessed by us) and the loss of a protecting arm of mussel banks. Not only could a loss of mussel banks have increased wave action in the

western, northern and southern sectors around Griend, the loss of cockle and mussel banks also involves: (1) an immediate loss of sediments during the mechanical shellfish harvests (see Fig. 4); (2) a lowering of the edges of the intertidal flats and thus an increase in tidal prism, and therefore leading to increased flood current velocities (cf. Dronkers 1984); and (3) a loss of the faecal and pseudofaecal pellet production of Edible Cockles and Blue Mussels, a product that is well known for its important role in deposition processes (Verwey 1952, Dankers *et al.* 1989, Oost 1995b, Hertweck & Liebezeit 1996). Composed of very fine material, the (pseudo-)faecal pellets produced by these filter-feeding bivalves behave hydrodynamically as sand grains and are able to 'catch' other sediments, thus leading to the formation of muddy sand flats (Waterloopkundig Laboratorium 1987).

Normally pellets of Blue Mussels disintegrate after a few days; faecal pellets of Edible Cockles may last longer. However, this does not mean that all clay contained in these pellets will be resuspended. Especially if the material has had some time to consolidate so that the water content decreases, the erodability is significantly reduced. Laboratory experiments showed an increase of the critical velocity before going in suspension to 40 cm/s after one day, and to 60 cm/s after 10 days (Creutzberg & Postma 1979). Sand grains within such a muddy environment will thus also be protected against going into suspension and being carried away.

Two slightly different scenarios can thus be envisioned to explain the observed changes in sediments from 1988 to 1992 and 1994: (1) The disappearance of the protective ring of faecal pellets-producing mussel banks induces sedimentary changes. The loss of a supply of material that makes the intertidal flats more erosion-resistant (faecal pellets), initiates a cascade of processes leading to stronger hydrodynamics on the intertidal flats that thereby became composed of coarse sediments. (2) The serious reworking of a large area of sediments by cockle-fishers during a period of storms ensured the instant loss of the original top layer of rather silty material leading to a coarser-grained intertidal flat that is, in view of the subsequent lack of bivalves and faecal pellet

production, also less erosion-resistant. According to the second scenario, cockle-fishing disturbance, rather than the removal of mussel banks, is the initiator of the seemingly irreversible changes that have taken place around Griend.

Whatever the precise scenario is that best accounts for our observations on changes in sediment characteristics around Griend, we suggest that the removal of the large stocks of filter-feeding bivalves in combination with the reworking of originally rather stabile sediments, the removal of a protective ring of mussel banks and an increase in tidal prism, have lead to a cascade of effects, to a 'negative biodepository spiral', leading to a more sandy habitat (Fig. 17). According to this hypothesis, the mechanical removal of the large filter-feeders kicks off sedimentary changes that then 'automatically' led to the disappearance of other filter-feeders (as will be documented below) that also produce biodepositorily important (pseudo-)faecal pellets, such as *Macoma* (Risk & Moffat 1977). In this scheme of things, the winter storms are not the causal agent. Storms (a perfectly normal phenomenon in the Wadden Sea anyway; see Fig. 16) are simply the executors of processes that have their beginnings in human perturbations of the apparently fragile balance of the Wadden Sea sedimentary systems.

4. MACROZOOBENTHOS

An important reason to embark on a detailed study of the *distributional ecology* (sensu Verwey 1952, 1954) of Knots rather than another shorebird species, was their well-known dietary specialisation for molluscs (see Piersma 1994). Molluscs, and especially bivalves, have a few great advantages over benthic groups such as polychaetes and crustaceans: (1) they live a rather stationary life, and thus aspects of their distribution relevant for shorebird predators are easier to describe, and (2) their protective armour (the shell), even when crushed in a muscular gizzard, leaves recognisable and measurable remains, for example in the faeces of the predators. It is thus possible to map, with relative ease, the distribution and the 'harvestability' (see next paragraph) of the prey as well as the distribution and diet of the predators. Both types of descriptive information are of critical importance during attempts to come to models that explain, or even predict, the occurrence of shorebird predators over a range of intertidal flats (see Zwarts *et al.* 1992, 1996, Piersma *et al.* 1995), and in studies of mortality, population dynamics and risk-taking behaviour of the invertebrate prey (e.g. van der Meer & Beukema 1997).

Many studies of predator-prey interactions are unsatisfactory in view of the fact that the precise conditions in which prey are susceptible to predation are unknown, or have been left unquantified. The research approaches established by L. Zwarts to handle problems of invertebrate prey availability for shorebirds feeding on intertidal flats have come some way towards the definitive research approach (see summaries in Zwarts & Wanink 1993, Ens *et al.* 1994). Some prey are buried in the sediment beyond reach of the bill (they are not *accessible*) and some may be too large to be swallowed (they are not *ingestible*). The overlapping parts of the accessible and ingestible fractions can be seen to represent the *available* prey. However, depending on current intake rate and/or energy requirements, some of these available prey may be too small to be *profitable*. The fraction of prey that is both available and profitable is called the *harvestable* fraction. The fraction of prey that is both profitable (above a minimum size) and ingestible (below maximum size) is called *suitably sized*. It is this fraction (the light box in the size-depth plot of

an imaginary bivalve in Fig. 18 bottom panel) that, ideally, has to be quantified for all different potential prey species in order to be able to predict intake rate (Fig. 18 mid panel) and thus explain diet and the local presence or absence of shorebird predators (see Piersma *et al.* 1995 for an example for Knots foraging near Griend). Note that Fig. 18 illustrates that factors other than harvestable biomass also affect the distribution of shorebirds (notably competitor densities, risk of predation by raptors, and the costs of thermoregulation). In the present report, maps of total densities and of the densities of

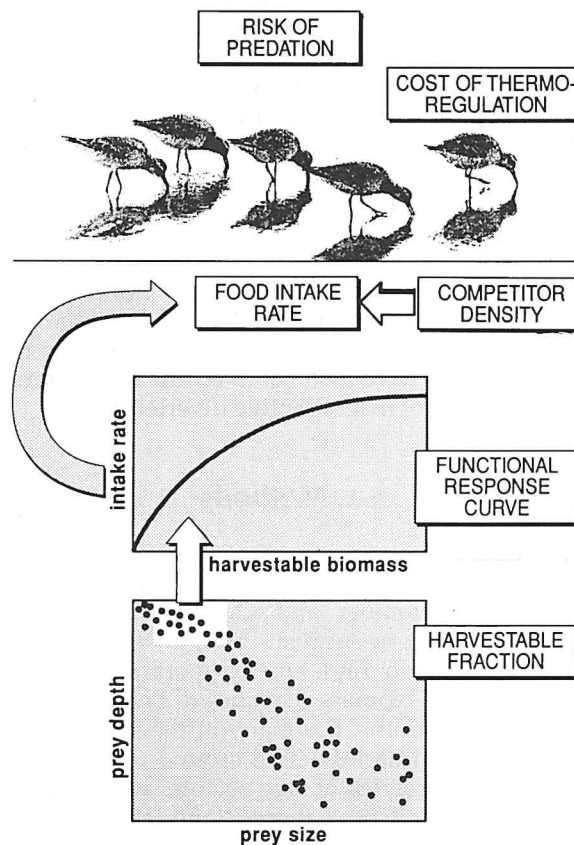


Fig. 18. Determinants of the quality of an intertidal feeding area for a bivalve-eating shorebird such as the Knot (modified from Piersma *et al.* 1993b). Note that not only prey densities, but also shell length (ingestibility) and the depth of living (availability) are critical measurements in assessments of the suitability of a potential feeding area.

suitably-sized bivalves (ingestible and presumably profitable) will be presented, along with data on the depth distribution of *Macoma balthica* and *Mya arenaria*. For *Cerastoderma edule*, a species that lives very close to the surface, ingestible densities are equal to available densities.

During our studies on the benthic invertebrates around Griend we therefore focussed initially on shellfish. In addition to recording numbers per unit area, for the molluscs we also measured their size distribution, and on a more limited temporal and spatial scale, their depth distribution. Depth distribution measurements are only relevant for the deep burrowing bivalves, especially *Macoma balthica* and *Mya arenaria*; *Mytilus edulis* and *Cerastoderma edulis* are always found on, or just under, the sediment surface, respectively. An added reason as to why the depth distribution of *Macoma* might be of relevance in the context of this report is the finding that, as a rule, in sandy sediments *Macoma* live deeper than in muddy substrates (P. de Goeij pers. comm.). The tendency of the intertidal flats around Griend to become coarser grained (Chapter 3), could thus affect the accessibility of the *Macoma*-stocks. From 1995 onwards, when we realised their potential as indicators of general environmental changes of the area, we have also sampled the other common species of macrobenthic invertebrates.

4.1. Methods

The data reported here were all collected in late summer/early autumn, in July (latter half only), August, September and October. Most data were collected in August. Piersma *et al.* (1993a) were unable to find any temporal effects on numerical or biomass densities of bivalves over these four months. For many of the subsequent analyses the intertidal area around Griend was divided in a series of five sectors: west, north, east, south and near shore-island, as indicated in Fig. 19.*

Densities

Up to 1992 the abundance of benthic animals was monitored by sampling the area along a

series of transects radiating from the island starting 100 m offshore from the high-tide mark and pointing in different directions. We were lucky enough to have mapped, in August-September 1988, all bivalves (but not the Mudsnaills *Hydrobia*) of the western and northern sectors around Griend before the cockle-fishing incident in late September, as sampling became impossible thereafter due to the reworking of sediments. Along these transects, series of cores were taken and sieved at fixed stations at intervals of 500 m (Fig. 19 top). If observations on the food and feeding of Knots made it necessary, we sampled additional stations. In 1993 this system was replaced by a mapping method using a fixed grid at 250 m intervals with sampling points (taking one core and sieving it) at each grid-intersection (Fig. 19 mid and bottom). To ensure that we would be able to compare the results of the benthic transect and grid-mapping programmes, in August 1993 the two exercises were carried out immediately after one another (Fig. 20).

From 1988 to 1992 sampling locations along transects were found by pacing out the distance with a calibrated step-length and a hand-counter, using a compass to walk in the appropriate direction. Locations away from the transects were found by crossreading the compass-bearings on the 'Brandaris lighthouse' in West-Terschelling, the house on poles at Griend, and if possible, the largest church-tower of Harlingen. From 1993 onwards the fixed and pre-determined positions were found with either a Philips 'AP-system' (using DECCA radio-beacons) or using hand-held GPS (Garmin).

As acknowledged in the previous chapter, in August-September 1989 we were still unable to sample the northern sector of the intertidal flats in view of the extensive reworking of these sediments during commercial dredging of *Cerastoderma* a year before. The layer of dead shells which normally occurs at a depth of 20-50 cm due to the activity of the polychaetes *Arenicola marina* and capitellid polychaete worms like *Heteromastus filiformis* (Cadée 1976, 1979), was still heavily mixed with the overlying soft sediments, making sieving impossible. However, it is likely that mollusc-densities were rather low there, and no Knots occurred in this segment in 1989.

*Fig. 19 and remaining figures of chapter 4 are placed after the text (pp. 33-67).

To sample *Cerastoderma*, *Macoma* and *Mya* we took 20 sediment cores of $1/56 \text{ m}^2$ down to a depth of 20 cm at each sampling station and sieved each of them over a 1-mm mesh. *Hydrobia* were sampled by taking 5 cores of $1/56 \text{ m}^2$ down to a depth of 3-4 cm and sieving them over a 0.5-mm mesh. The content of each core was put into a separate identifiable plastic bag and stored frozen until laboratory treatment. In the fixed grid-mapping approach from 1993 onwards, only one sediment core of $1/56 \text{ m}^2$ for larger animals and one of $1/126 \text{ m}^2$ for *Hydrobia* each, were taken at each point, but sampling depth did not change. In 1993 we started counting not only the bivalves but also some of the worms and crustaceans retained on the 1-mm mesh, although only the bivalves were collected for subsequent processing in the laboratory. From 1995 onwards we tried to count all animals retained on the 1 mm mesh, but in view of the depth of sampling some of the larger fauna, notably adult Lugworms *Arenicola marina*, soft-shell clam *Mya arenaria* and Razor Clams *Ensis directus*, would have been missed. Animals were identified and named according to Hayward & Ryland (1995).

Size distributions and biomass determinations

In the laboratory, the molluscs in each bag were counted and measured to the nearest mm (*Cerastoderma*, *Macoma*, *Mya*) or nearest 0.5 mm (*Hydrobia*). The maximum length of the bivalve-hinges was measured on mm-paper or with vernier calipers. The lengths of *Hydrobia*-shells were measured under a binocular microscope with a micrometer mounted in the eyepiece. In the bivalves, the soft parts were then separated from the shell (easy after freezing) and shells and meat of different sized bivalves from one station were put in crucibles and dried in a ventilated drying oven at 55-60°C to constant mass. For *Hydrobia*, entire animals were dried per length class. The dry masses of the crucibles containing the entire snail, the bivalve-meat, or the bivalve-shells were then weighed and incinerated at 550°C for two h. After cooling in a dessicator, the crucibles plus content were reweighed and finally the empty mass of the crucibles were obtained. In this way we determined the dry mass (DM), ash mass and ash-free dry mass (AFDM) of the meat (DM_{meat} , $\text{AFDM}_{\text{meat}}$) and shell (DM_{shell} , $\text{AFDM}_{\text{shell}}$) fraction in bivalves, and of the

entire animal in *Hydrobia* (DM_{total} , $\text{AFDM}_{\text{total}}$) (see Dekinga & Piersma 1993, Piersma 1994 for terminological conventions).

Availability of bivalves

The depth of *Macoma* and *Mya* was determined by cutting up cores of $1/56 \text{ m}^2$ in thin vertical slices until one was encountered. The distance between the upper edge of the shell and the surface was then measured (see front cover and Zwartz 1986:fig.1 illustrations). We checked whether any sediment was lost from the surface of the core by plugging in a 'surface indicator' before taking it. In case of sediment loss, we corrected the measured depths accordingly. We usually aimed for 50 individuals per site and per species. This work was usually undertaken by small teams working at a certain location for entire low water periods (Fig. 21).

After being located, and the depth measured, individual bivalves were assigned to depth intervals of 0.5 cm above a depth of 5 cm, and of 1 cm below 5 cm depth. In the laboratory, $\text{AFDM}_{\text{meat}}$'s of the individual bivalves were measured. The locations where depth samples were taken in the course of the studies (August-October 1988-1996) are summarised in Fig. 22. Only in 1994 and 1996 (the first years with significant numbers) was the depth distribution of *Mya* measured a few times.

4.2. Results

Transect versus grid mapping methods

Given that, at each sampling site along the transects investigated in 1988-1993, a fixed number of 20 deep cores for sieving over a 1 mm mesh, and 5 shallow cores for sieving over a 0.5 mm mesh were taken, rather than single cores at each sampling site during the grid method (Fig. 20), the relative sampling effort close to the island (or on the highest parts of the intertidal flats) had been far larger during transect sampling than during grid-mapping. As distribution patterns of benthic animals vary with respect to height or distance from a shore (e.g. Kristensen 1957, Dankers & Beukema 1983), the two methods might give different results when it comes to average density figures per size category per sector. The calibration exercise in August 1993 allowed to check for this bias.

As expected, for *Cerastoderma* the small cohort is better represented in the results of the transect method than in the results of the grid method (Fig. 23). This effect is caused by the differential settlement of spat on the highest parts of the intertidal area, and is even more visible for *Macoma* (Fig. 24). As we aim to compare average densities of benthic species per sector for a series of years, it is pertinent to ask whether this bias in size distributions during transect sampling compared to grid sampling is affecting the density or biomass estimates. Figure 25 (top) shows that for *Cerastoderma* density and size trends apparently cancel each other out with respect to biomass at the level of sectors, and that there is no need to adjust the earlier transect density values to those obtained during grid-mapping. However, for *Macoma* the grid method clearly yields higher biomass values than the transect methods (due to a relative excess of small-sized and light-weight *Macoma* closer to the island during the latter method). Accordingly, in the summary presentation (Fig. 41), densities of *Macoma* in 1988-1992 have been corrected upward to the level obtained during grid-mapping.

Cerastoderma edule, the Edible Cockle

The Edible Cockle is a suspension-feeding bivalve that lives just below the surface of the sediment and pumps water over its gills via the wide short siphons fringed with a ring of tentacles (Fig. 26). Rather than burying deeply, *Cerastoderma* tries to ward off predators by means of a robust and rotund shell. In early September 1988, the western, northern and eastern sectors contained high densities (over a 100/m²) of adult ((2 year) *Cerastoderma*, reaching biomass values as high as 70 g AFDM_{meat}/m² (Fig. 27, Piersma *et al.* 1993a). In view of the large size of these *Cerastoderma* (Fig. 29), only a small proportion of this biomass (less than one percent, in fact) was suitable for ingestion by Knots. The mechanical harvest described in Chapter 2, in combination with the epibenthic predators that continued to feed on any remaining cockles, was very effective and hardly any large *Cerastoderma* remained to be found in 1989. Spatfall of *Cerastoderma* was also low (Fig. 27), and low rates of recruitment have been the rule ever since. The northern sector (except for a strip close to the island) was pretty much abandoned by the Edible Cockles, and from 1991 onwards

the largest densities were found in the eastern sector (Figs. 27 and 28).

The grid-mapping carried out since 1993 allows for rather more detailed observations on spatial distribution (Fig. 28). Even though highest densities tended to occur in the eastern sector, the precise location of the areas with *Cerastoderma* varied from year to year. For example, the cockle-areas within the eastern sector in 1993 and 1996 were almost mutually exclusive (Fig. 28). Not only does the spatial distribution of Edible Cockles vary from year to year, so does the size distribution of those present (Fig. 29). In 1988, when we started our studies, the great majority of animals was large and three or four year old. In view of the low recruitment, comparable stocks of large adults have never occurred again. It also strikes the eye that the size attained by the settling cockles varied considerably (Fig. 29). For example, in 1990 settlers were relatively large (7-10 mm), whereas a year later they were rather small (mostly 2-7 mm). Knots are only capable of eating the small *Cerastoderma*, and it comes as no surprise that the numerical and biomass densities of suitably sized animals (Fig. 30) was rather lower than that of the whole population (Fig. 28), although the general distribution pattern bears much resemblance.

The temporal trends in the abundance of Edible Cockles around Griend are summarised in Fig. 31. The sectors showing the highest stocks in 1988 (west and north), which are also the ones that were affected directly by shellfisheries and showed the largest sediment changes, showed no recovery over the period 1989-1996. In the eastern sector densities also decreased, but to a lesser extent. In the southern sector densities were low throughout, but showed a peak in 1992-1993. The biomass figures for suitably sized *Cerastoderma* were never very high, and highly variable from place to place and from year to year (Fig. 31).

Mytilus edulis, the Blue Mussel

Like the Edible Cockle, the Blue Mussel cannot bury deeply and tries to avoid predation by building a strong shelly armour. It is also a suspension-feeder with short wide siphons (Fig. 32), but rather than occurring in the top layer of the sediment, it occurs in dense congregations *on top of* the sediment, in the so-called mussel banks. Mussel banks have traditionally been

found on many parts of the intertidal flats around the island of Griend (Fig. 33), and formed a semicircle around the western flats when we started this study in 1988 (Fig. 5). As has been documented in Chapter 3, the mussel banks were removed in 1989-1990, and no mussel banks remained in August 1991 when large numbers of a formerly common predator of Blue Mussels, the Common Eider *Somateria molissima*, were found dead on the beaches of Griend. During the period of study, only in 1994 two small mussel banks of 3 ha each were temporarily established south and southeast of the island. We collected some clumps of mussels and the size distribution of the Blue Mussels present is given in Fig. 34. A single year class (the one of summer 1994) was present, with a median shell length of 11 mm, and a range of 5-19 mm. These mussel banks were fished upon in the latter half of 1994 and had disappeared completely by early August 1995. Just before the time of writing, during the summer of 1997, two small patches of Blue Mussels settled north and southeast of Griend.

Macoma balthica, the Baltic Tellin

Baltic Tellins are deep burying bivalves with a pair of thin extensible siphons, a very long one to inhale, and a much shorter one to exhale (Fig. 35). Baltic Tellins have the characteristics of a deposit-feeding bivalve, but in many occasions they may suspension-feed as well (Kamermans 1992). They are usually buried rather deeply in the sediment, extending the inhalent siphon over the substrate only if feeding on the algae and detritus sitting on the sediment surface.

In 1988 densities of *Macoma* were highest in the northern sector (Fig. 36). Overall, densities became higher further away from the island (Fig. 36). In the north densities collapsed after the cockle-dredging incident of 1988, and densities comparable to the one found in 1988 were only seen in the eastern sector, rather far away from the island, in 1991 and 1992. The rather more detailed mappings carried out in 1993-1996 confirm the pattern of rather larger biomass values further away from the island (Fig. 37); the numerical densities seem to be rather more constant than biomass densities over larger units of area. Following a gradual increase since 1989, densities in the southern sector started to equal those in the eastern sector. West and north of Griend, *Macoma* remained

scattered and rare in the years 1993-1996 (Fig. 37).

The size distribution of the *Macoma* population varied greatly from year to year (Fig. 38). Recruitment was quite low throughout, but higher than average in 1989, 1991 and 1994. The year 1995 was an all-time low with regard to both recruitment and overall densities. As most of the *Macoma* present were actually of the suitable size (3-18 mm) for ingestion by Knots, the maps portraying the densities of suitably sized *Macoma* (Fig. 39) closely resemble those giving total densities (Fig. 37).

The accessibility of Baltic Tellins varied predictably with time of the year, but rather unpredictably from year to year (Fig. 40). The proportion of the suitably sized *Macoma* that were accessible to Knots in August varied between 13 and 47%, but in all three years for which data are available (1988, 1989 and 1991), the proportions decreased with time of the year, *Macoma* burying deeper as autumn came. From 1993 onwards densities of *Macoma* were usually too low to be of importance as prey for Knots, and thus to be depth sampled.

The temporal trends in the abundance of *Macoma* on different parts of the intertidal flats around Griend are summarised in Fig. 41. As in *Cerastoderma*, the decreases were most pronounced in the western and northern sector and continued over a longer period of time. The eastern and southern sectors also showed decreases, but only from 1992 onwards is this downward trend really striking. In 1995 the lowest densities of *Macoma* occurred, with a slight rebound in the last year of study.

Mya arenaria, the Soft-shell Clam or Sandgaper

The Soft-shell Clam or Sandgaper is a typical suspension-feeder that lives deeply buried in soft sediments extending a thick combi-siphon (the pipes representing inhalent and exhalent siphons merged into a single chimney) to the surface of the sediment (Fig. 42). Keeping away from the dangerous surface of the sediment after reaching a certain size (ca. 25 mm), Sandgapers cannot dig very well if accidentally ending up on the surface (Checa & Cadée 1997), and their shell is rather soft. Those that survive the onslaughts of long-billed predatory waders over the first few years of life (Zwarts & Wanink 1984), can get rather big and rather old.

Around Griend, *Mya* must have been very

rare in the first half of this study. At least, only very few (some small animals in 1991) were picked up by the transect-based benthic surveys. When we started grid-mapping in 1993, here and there a single *Mya* was found, but nowhere more than one or two per deep core (Fig. 43). In 1994, however, all of a sudden we found quite good densities of *Mya*-spat in areas south and east of Griend, and these resources were immediately capitalised upon by the Knots (see Chapter 5). Some of these *Mya* remained in 1995, having grown over the intervening year (Fig. 44), but densities were boosted again by another major spatfall in 1996, this time predominantly east of Griend (Fig. 43). With their rather fast growth, only the recently settled *Mya* are of sizes (and live at depths, see Zwarts & Wanink 1984) suitable for Knots. Therefore the distribution maps of suitably sized *Mya* (Fig. 45) only show good numbers and biomass values in the two years with spatfall, 1994 and 1996. Note, however, that first-year *Mya* live quite close to the surface (Fig. 46) and are accessible for the greater part by feeding Knots.

The summary graphs in Fig. 47 nicely tell the story of the peaked appearances of *Mya* near Griend: a few in 1991, first-time settlement in large numbers in 1994, and another invasion in 1996. Only in these two years with good spatfall were any *Mya* available for ingestion by Knots.

Hydrobia ulvae, the Mudsnaill

Mudsnaills are tiny gastropods living on or just below the surface of intertidal soft sediments (Fig. 48). During certain tides whole populations of Mudsnaills may make massive movements by becoming buoyant (or rather floating attached to the undersurface of the water, Newell 1964) and allowing themselves to be carried on or off particular flats. In spite of this potential for rapid movements, the distribution pattern and densities of Mudsnaills present around Griend is fairly predictable (Figs. 49 and 50; note that we missed the opportunity to sample *Hydrobia* quantitatively, as we only started doing it after the cockle-fishers had their go at the northern and eastern flats). In all years, Mudsnaills occurred in the highest densities (often several 1000 animals/m² on the highest parts of the intertidal flats around Griend, more or less over a 'ridge' extending east-northeast from the island. In many years good densities of *Hydrobia*

were also found in the southern sector, but never very far away from the island.

The size distributions show some variations from year to year, but rather less than the preceding bivalve species (Fig. 51). In all years there seems to be a fair recruitment (*Hydrobia* showing up as 1-3 mm long individuals), but in some years some of the two-year olds have survived (very notable in 1990, a year with low recruitment). As all size classes should be suitable for ingestion by Knots, the temporal changes in overall densities give a fair description of what matters for a predator like the Knot (Fig. 52). Reasonable biomass densities of several g AFDM/m² only occurred in the eastern and southern sectors. Between 1988 and 1995 the densities varied with a factor of about three in the most predictable area, the eastern sector.

Other benthic species

One of the most common polychaete worms in the Wadden Sea belongs to the Nereidae family and is called the Ragworm *Nereis* (*Hediste*) *diversicolor* (Fig. 53). *Nereis* leads a crawling life, usually beneath the surface of the sediment, and is only rarely fed upon by Knots. Densities around Griend were highly variable from year to year (as measured from 1993-1996), even though the distribution was rather predictable (Fig. 54). Densities were highest over most of the eastern and southern sectors, with somewhat smaller densities in a ring around the island, 1-2 km offshore. In 1996 *Nereis* occurred in peak numbers, showing densities as high as 1000 animals/m² in some areas.

A polychaete worm of rather similar general appearance as the Ragworm (though more lightly colored, of a 'stiffer' built, and behaving more 'wriggly') is the Catworm *Nephtys hombergi* (Nephtyidae), a predator of small polychaetes. Over the period of study, *Nephtys* was never very common (Fig. 55), occurring widely but thinly over much of the area, with some tendency to occur rather far offshore in the sandiest parts of the intertidal flats.

Scoloplos armiger is a small orange coloured polychaete worm of the Orbiniidae family, fed upon by Catworms and probably a favourite prey of waders like Dunlins *Calidris alpina*. We only started recording their abundance in 1995 in concert with more wide-ranging benthic surveys in the western Dutch Wadden Sea. *Scoloplos* was widely distributed over the intertidal

flats around Griend (Fig. 56), but with remarkable differences between the two years that they were mapped. In 1995 *Scoloplos* was absent from the northwestern corner of the intertidal flats, but had its stronghold there in 1996.

Even thinner polychaete worms, of a blood-red colouring, are *Capitella capitata* and *Heteromastus filiformis*, both of the Capitellidae family. We have not identified them to species, but rather tried to record numbers of individual blood-red worms as best as we could (capitellids often break during sieving). They occurred widely around Griend (Fig. 57), with highest

densities in the western sector in 1995, and highest densities in the 'far' east-northeast in 1996.

A tiny but striking crawling creature on the sandiest parts of the intertidal flats is a small amphipod crustacean of the Haustoriidae family, *Urothoe poseidonis*. *Urothoe poseidonis* occurred in high numbers in 1995 and in low numbers in 1996 (Fig. 58), mainly north of Griend. In 1995 their densities in some areas exceeded a remarkable 1000/m². We only rarely encountered single specimens of *Corophium* (another amphipod) on the Grienderwaard.

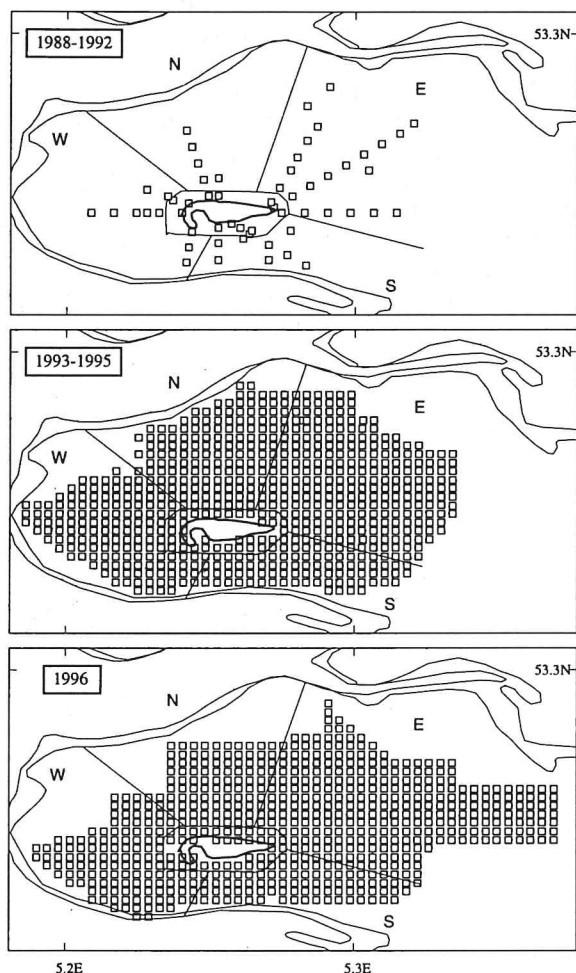


Fig. 19. Distribution of the benthos sampling points on the intertidal area around Griend in 1988-1996. Note that up and until 1993 we sampled along transects rather than using the grid-mapping approach (see text).

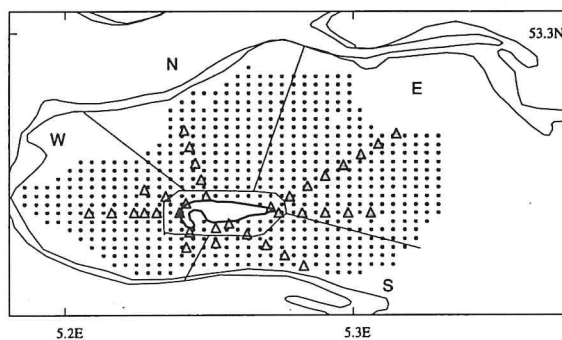


Fig. 20. Comparison of the geographical extent of the two benthos sampling strategies (points along transects indicated with triangles used in 1988-1993, and grid mapping indicated with dots used from 1993 onwards) for the intertidal area around Griend. The two methods were compared in 1993. The transect points (triangles) were sampled from 8-13 August and the grid (dots) was covered from 19 August to 4 September.



Fig. 21. Illustrating the depth sampling of *Macoma* and *Mya* on the intertidal flats around Griend (photographs by Theunis Piersma [top] and Rik Kuiper [bottom]).

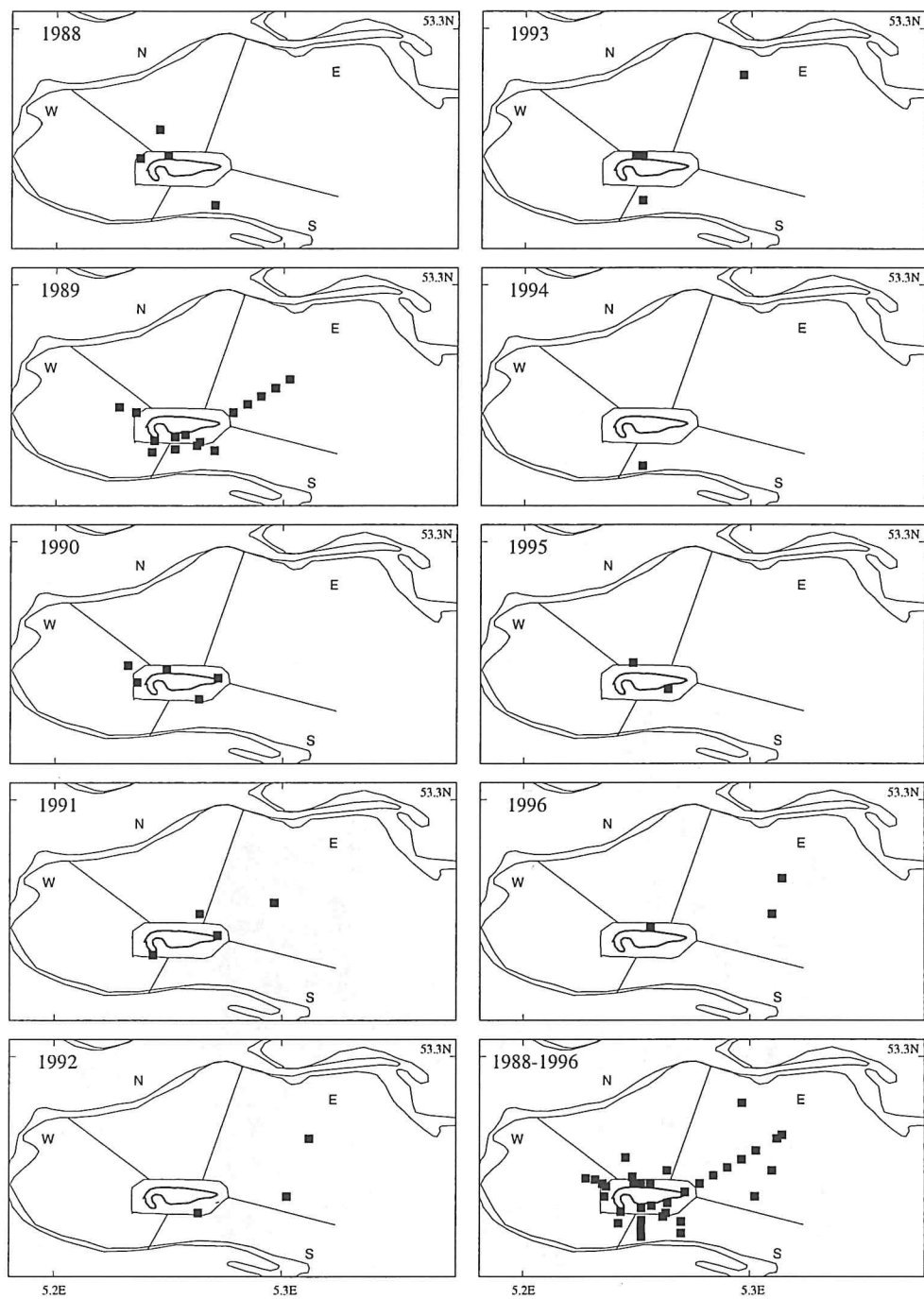


Fig. 22. Summary of the stations where the depth distribution of buried bivalves (especially *Macoma*) was measured from 1988-1995.

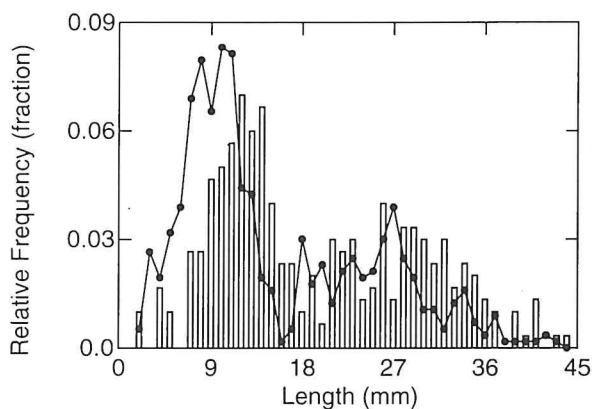


Fig. 23. Comparison of the size distribution of *Cerastoderma edule* sampled according to the transect (dots) and grid (bars) methods in August 1993 (based on 565 measured *Cerastoderma* with the transect method and 300 with the grid method).

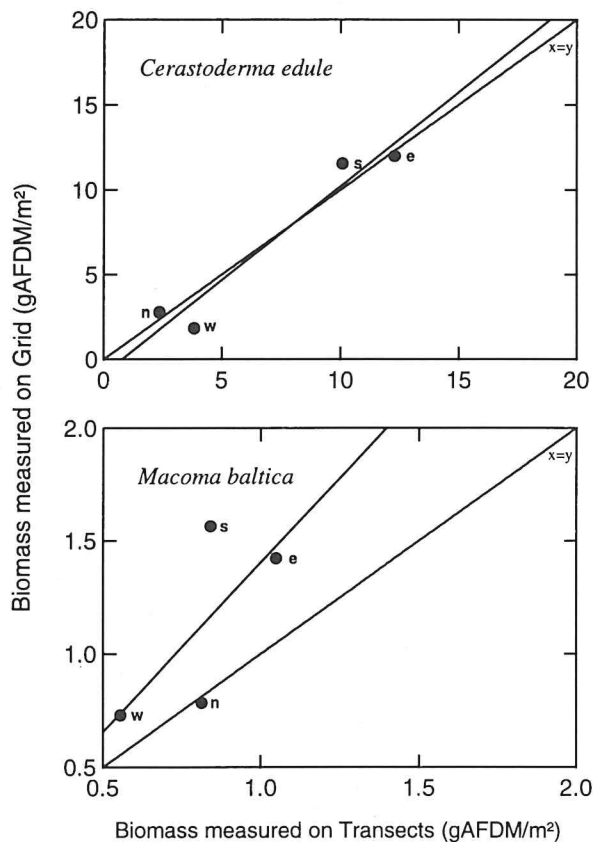


Fig. 25. Comparison of the average biomass values (in AFDM (g)/m²) in the different sectors around Griend sampled according to the two different methods. (A) *Cerastoderma edule* and (B) *Macoma balthica* (B). For *Cerastoderma* Y (grid) = $1.106 \cdot X$ (transect) - 0.86 ($r^2=0.94$), and for *Macoma* $Y=1.497 \cdot X - 0.09$ ($r^2=0.50$).

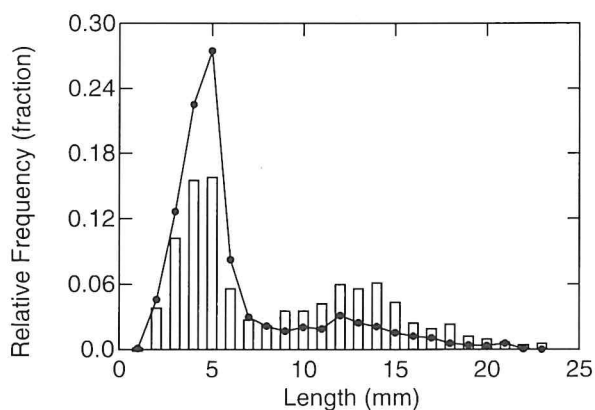


Fig. 24. Comparison of the size distribution of *Macoma balthica* sampled according to the transect (dots) and grid (bars) methods in August 1993 (based on 1937 measured *Macoma* with the transect method and 735 with the grid method).

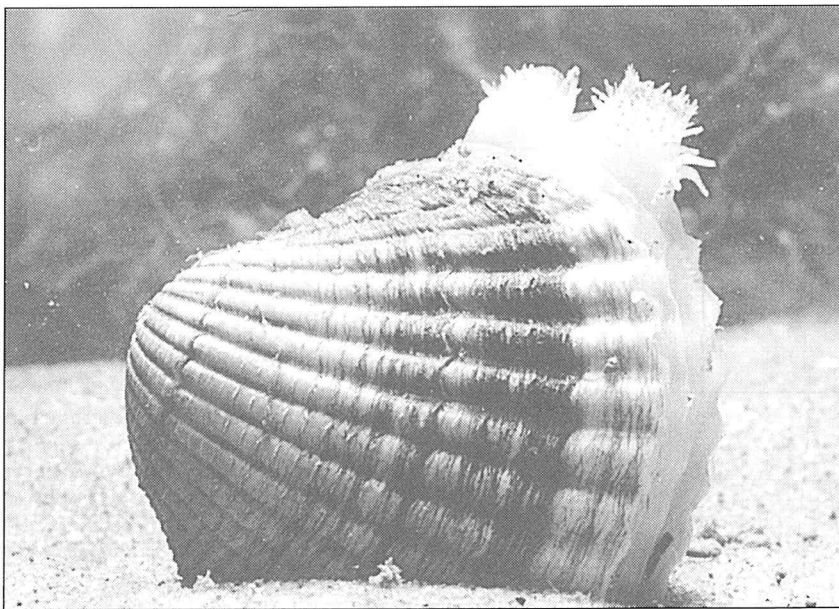
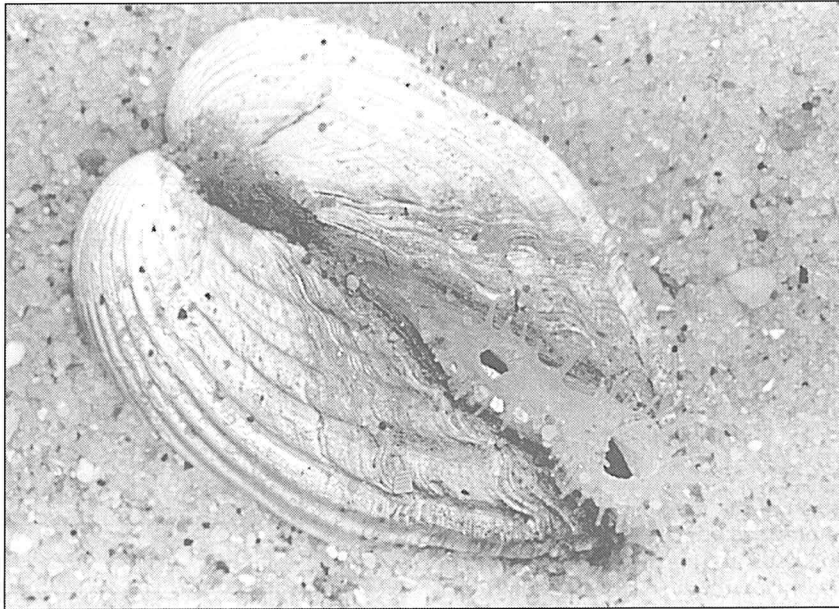


Fig. 26. Top and sideways views of half-buried adult Edible Cockles *Cerastoderma edule*
(photograph by Jan van de Kam)

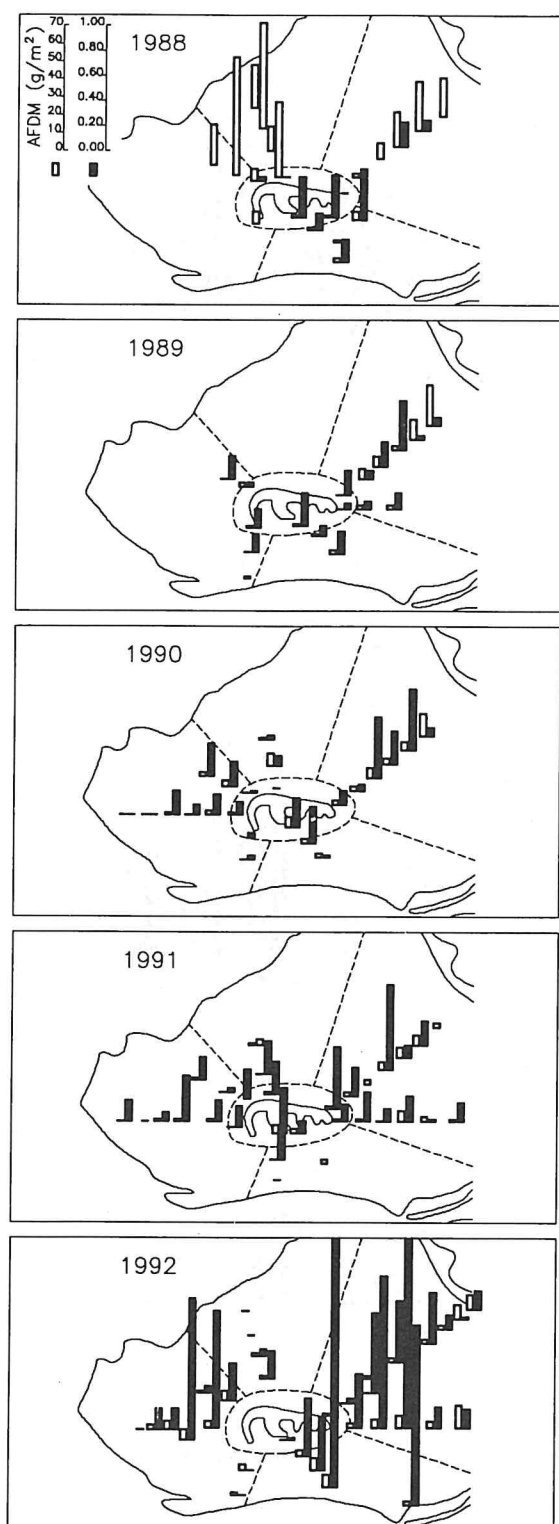


Fig. 27. Spatial and yearly variation in the overall abundance of *Cerastoderma edule* near Griend in the period 1988-1992 (from Piersma *et al.* 1993a). At each sampling station 20 cores of $1/56 \text{ m}^2$ were taken. The white left bar indicates total biomass of *Cerastoderma*, the black right bar the biomass of ingestible (and profitable) cockles (those of length suitable for ingestion by Knots: 3-14 mm).

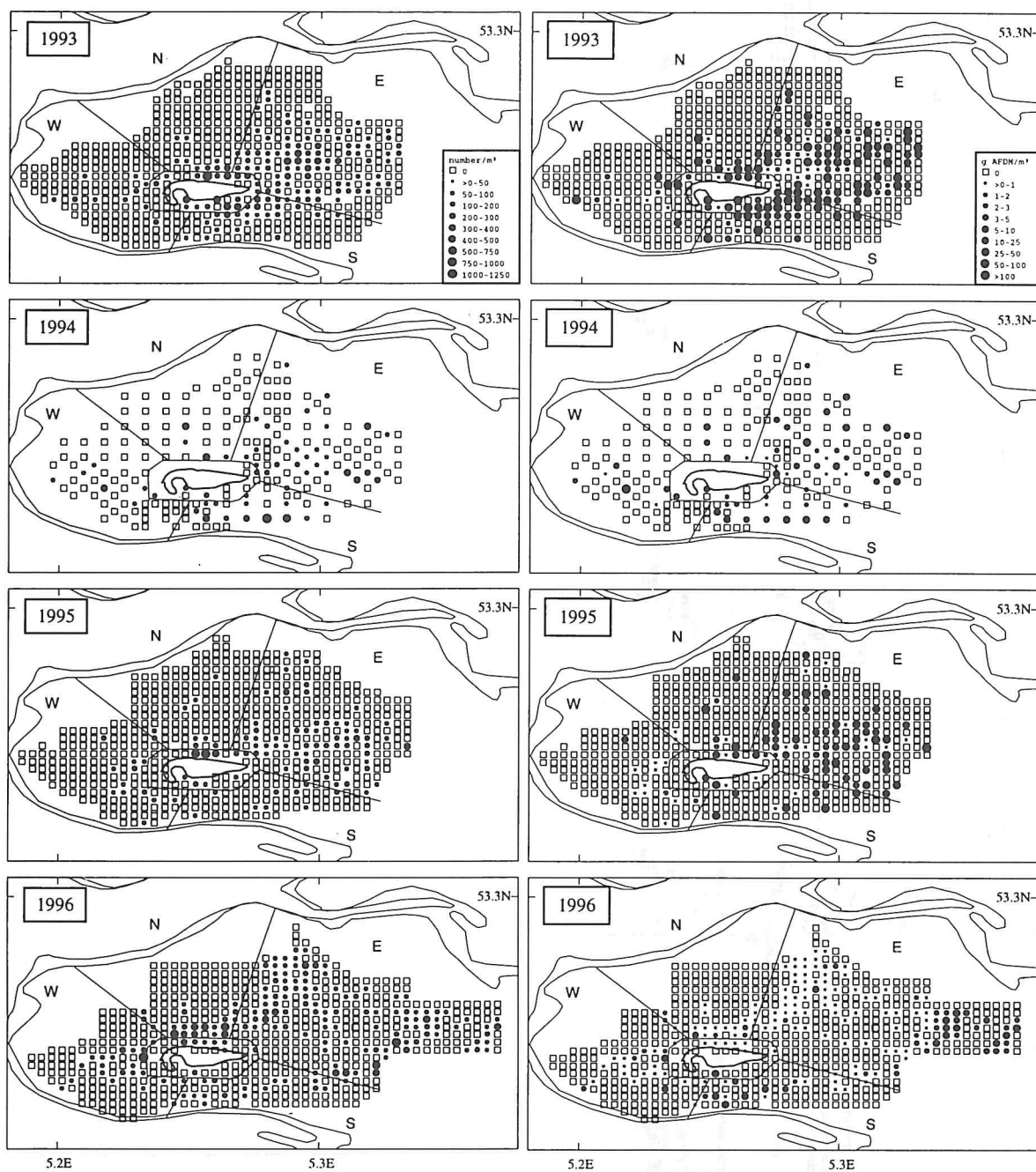


Fig. 28. Spatial variation in the total densities (in numbers [n/m^2 , left] or biomass [AFDM (g)/ m^2 , right]) of *Cerastoderma edule* around Griend in 1993-1996.

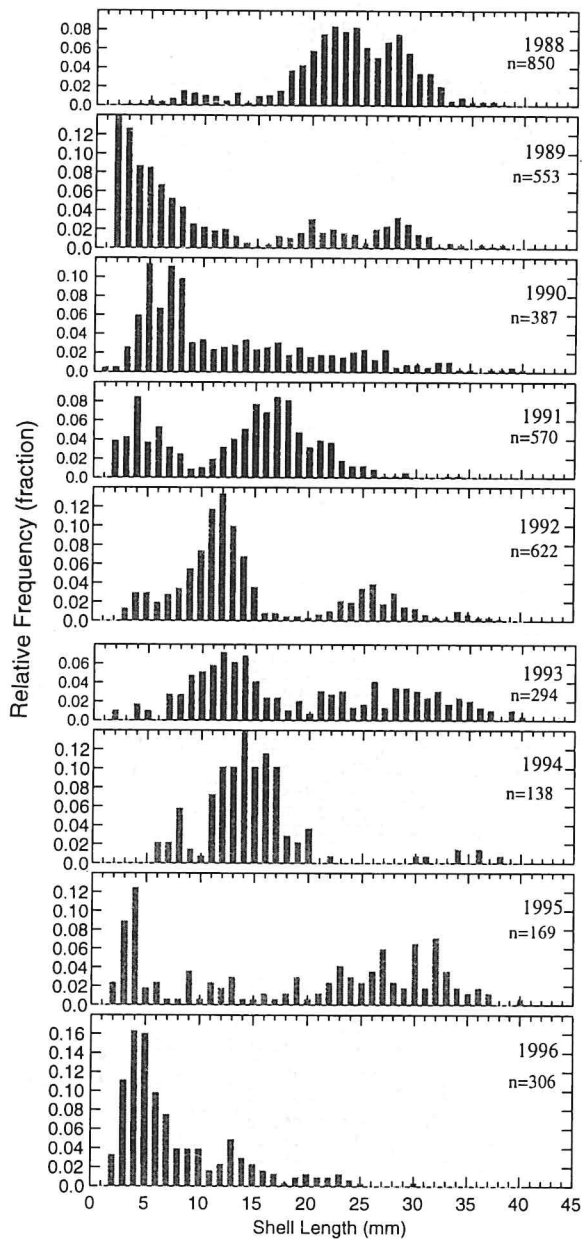


Fig. 29. Long-term changes in the size distributions of *Cerastoderma edule* as determined in August-September on the intertidal flats around Griend. Note that from 1988-1992 we employed the transect methods, rather than the grid method used since. At least in 1993, the transect method gave a slight predominance of smaller cockles (see Fig. 23).

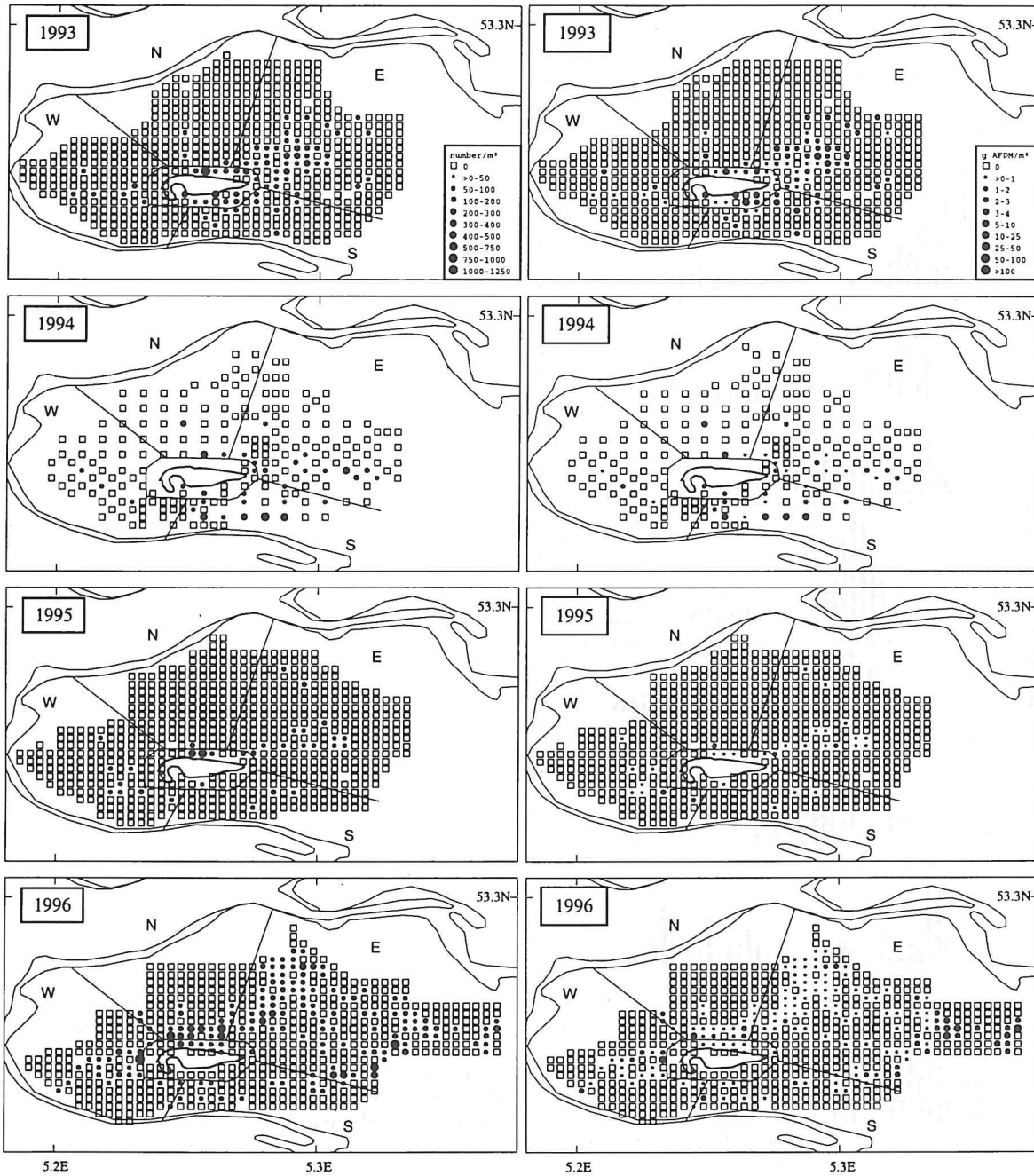


Fig. 30. Spatial variation in the densities (in numbers [n/m^2 , left] and biomass [AFDM (g/m^2 , right]) of suitably sized (3-14 mm long) *Cerastoderma edule* around Griend in 1993-1996.

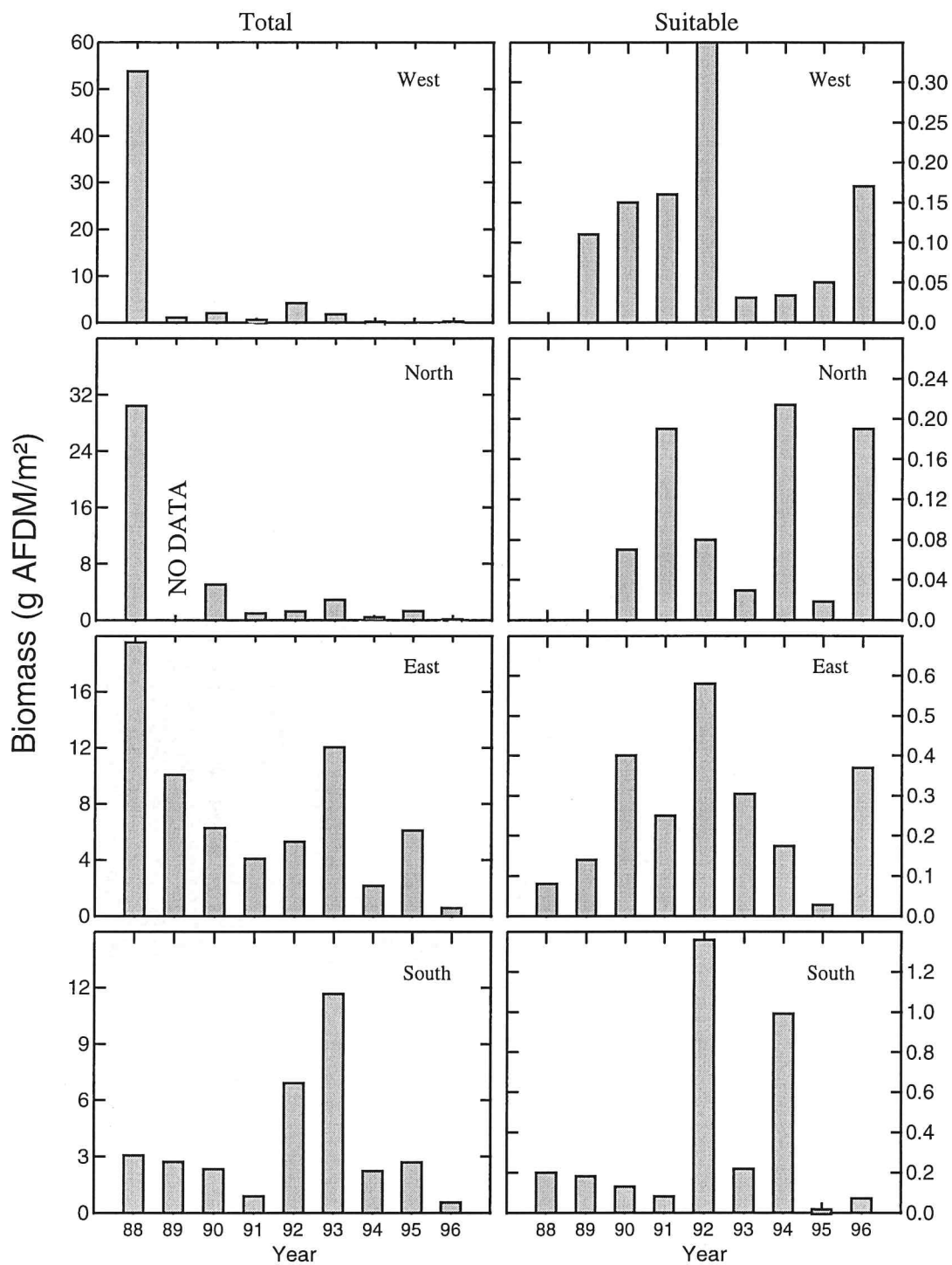


Fig. 31. Summary statistics (four double panels with histograms) of the changes in biomass densities of *Cerastoderma* in the different sectors around Griend in 1988-1996. Total biomass values are given at left, biomass densities of suitably sized *Cerastoderma* at right.



Fig. 32. Photograph of Blue Mussels *Mytilus edulis* (photograph by Jan van de Kam)



Fig. 33. Photograph of mussel banks near Griend in the early 1970s. Note the warden's house and the beacon in the distance. (photograph by Jan van de Kam)

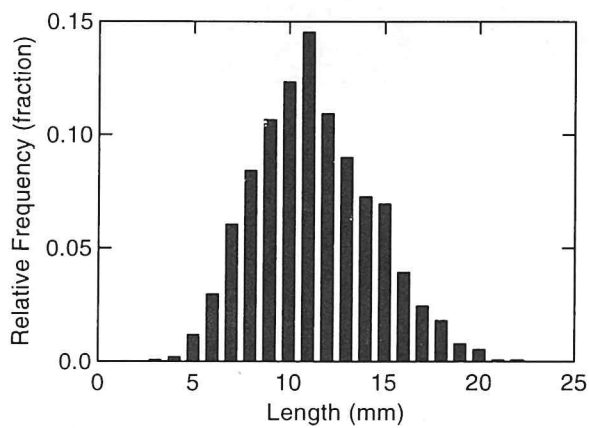


Fig. 34. Size frequency distribution of *Mytilus edulis* collected on the two small mussel banks along the Blauwe Slenk south of the island of Griend on 5 September 1994 ($n = 1557$).

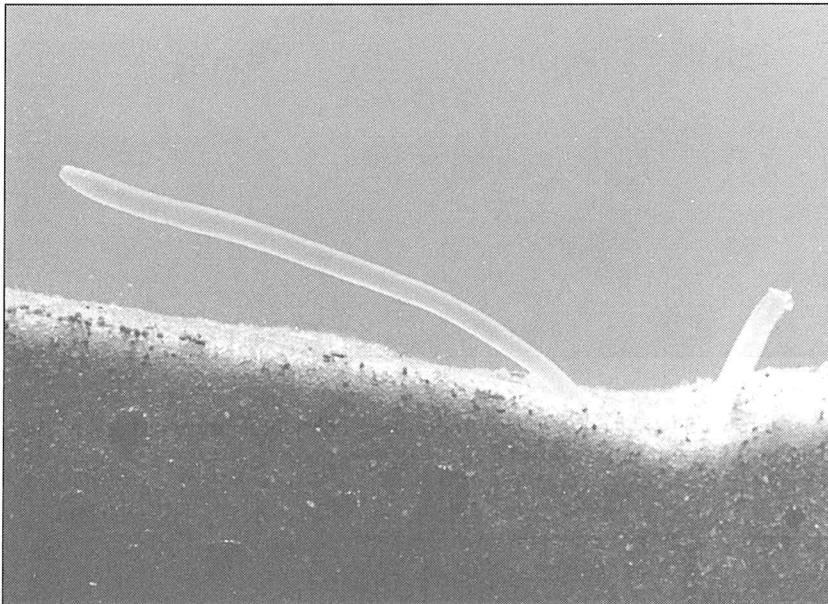
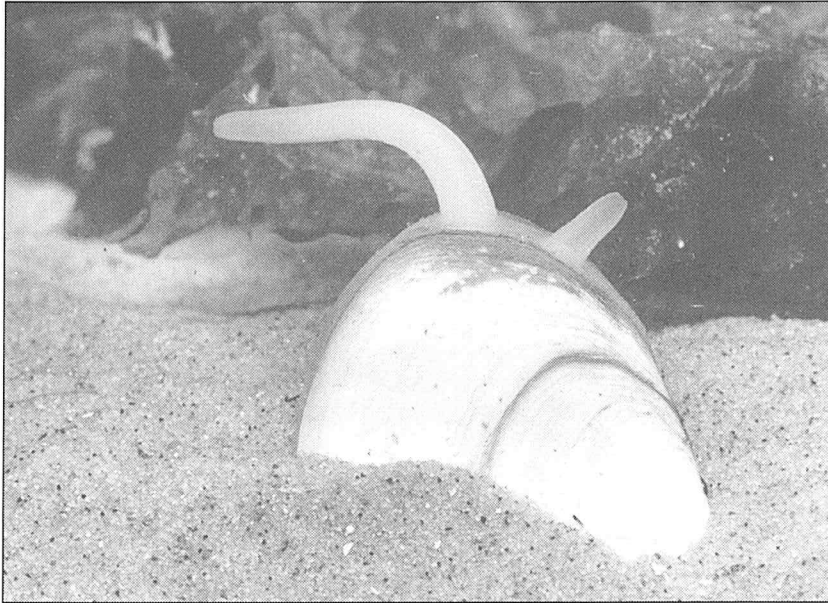


Fig. 35. Half-buried (top) and deeply buried Baltic Tellins *Macoma balthica*, with their inhalent (left tubes) and exhalent siphones (right tubes) extended. (photograph by Jan van de Kam)

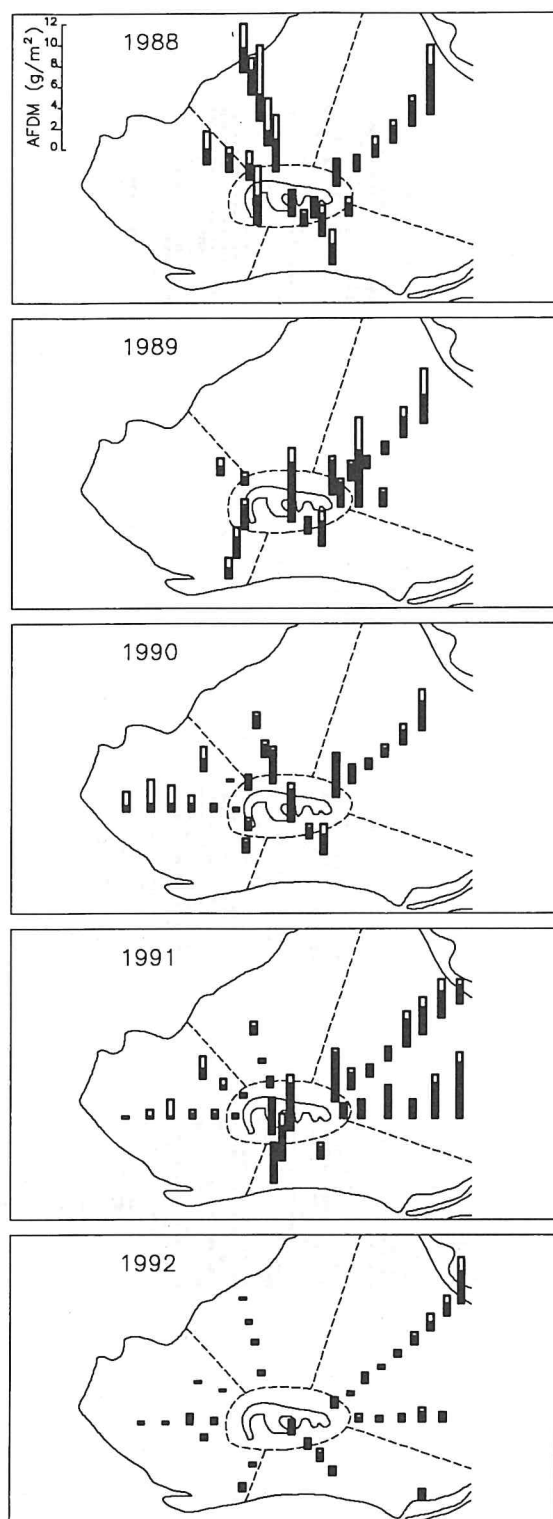


Fig. 36. Spatial and yearly variation in the overall abundance of *Macoma balthica* near Griend in the period 1988-1992 (from Piersma *et al.* 1993a). At each sampling station 20 cores of $1/56 \text{ m}^2$ were taken. The total bar indicates total biomass, the hatched part of the bar the biomass of ingestible (and profitable) tellins (those of a length suitable for ingestion by Knots: 3-18 mm).

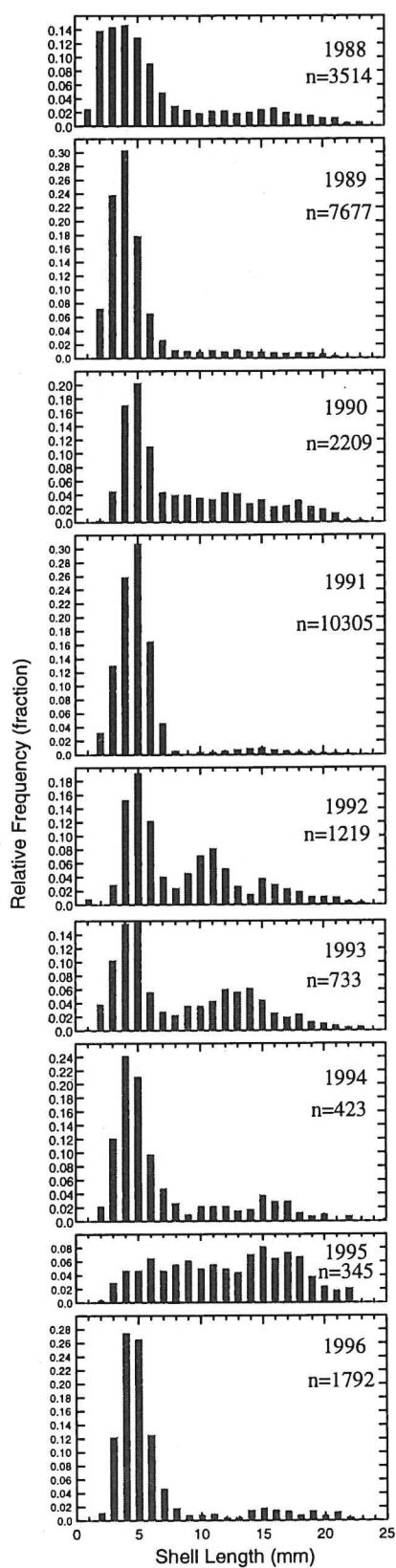


Fig. 38. Long-term changes in the size distributions of *Macoma balthica* as determined in August-September on the intertidal flats around Griend. Note that from 1988-1992 we used the transect methods, instead of the grid method used since. The transect method gives a predominance of the smaller *Macoma* (see Fig. 23).

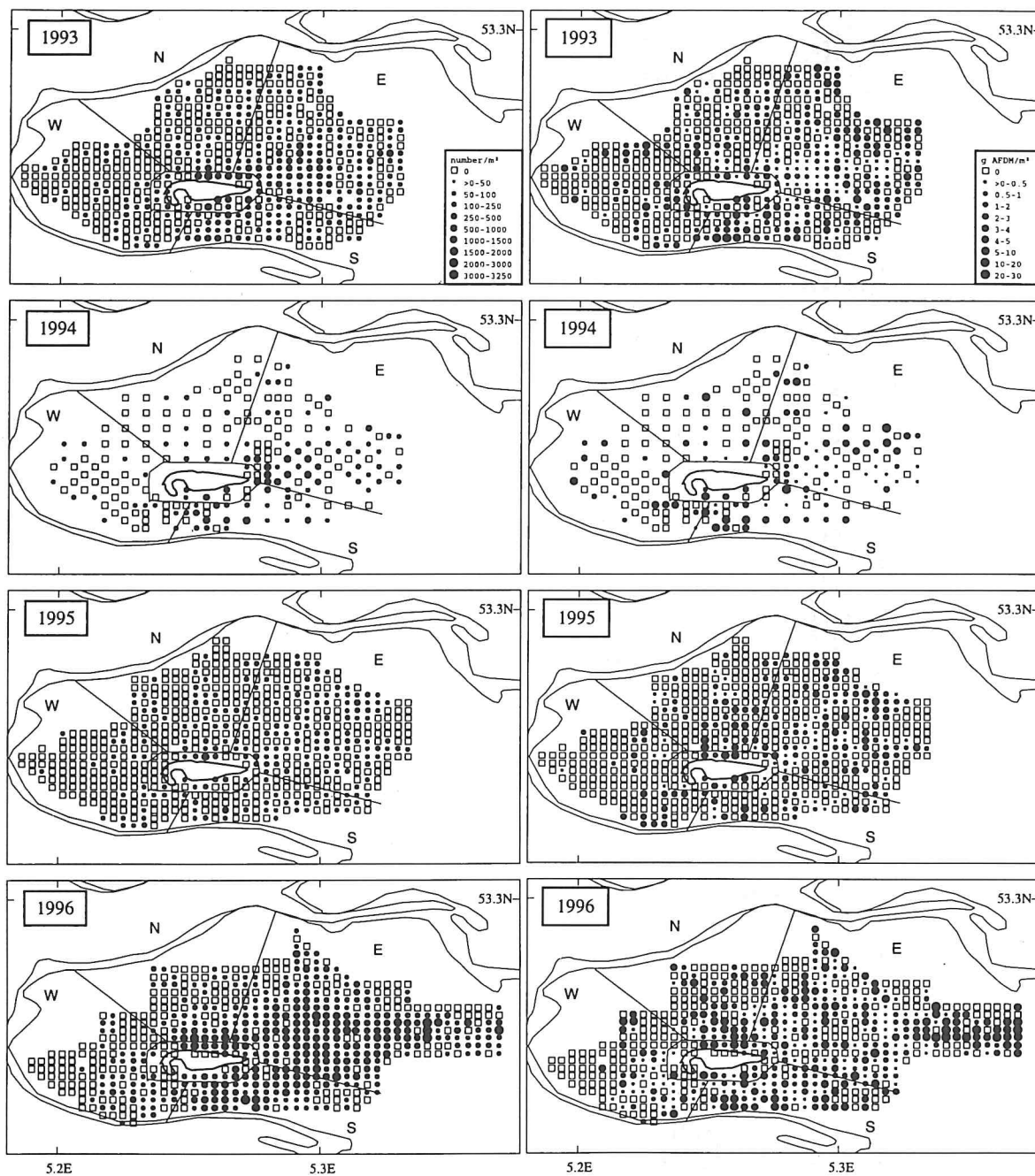


Fig. 39. Spatial variation in the densities (in numbers [n/m^2 , left] and biomass [AFDM (g)/ m^2 , right]) of suitably sized (3-18 mm long) *Macoma balthica* around Griend in 1993-1996.

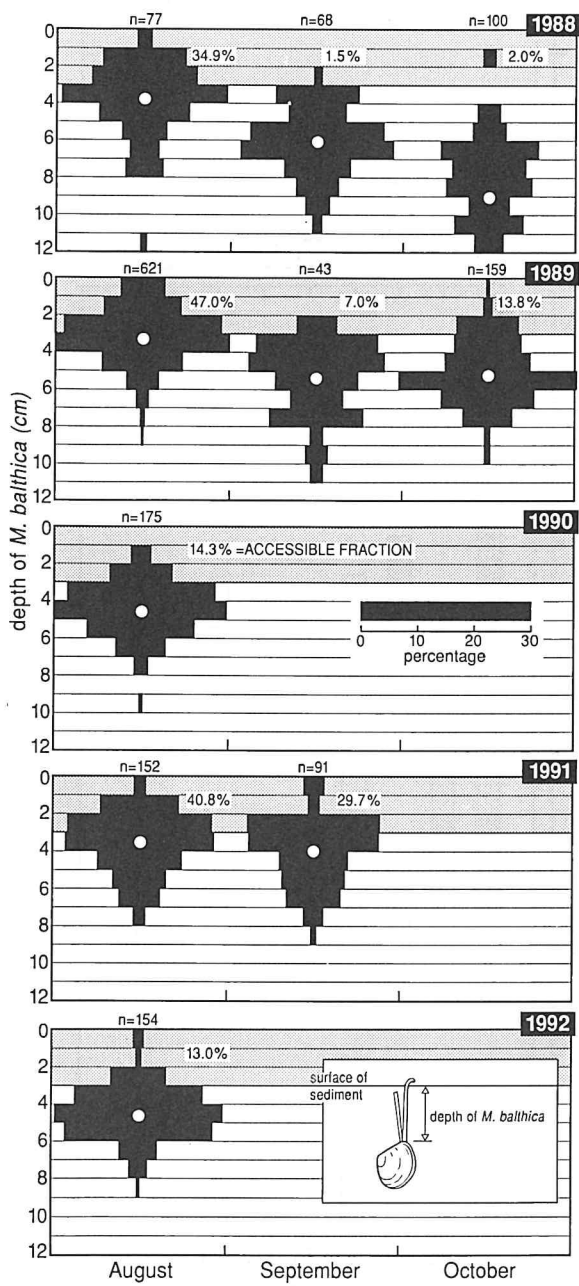


Fig. 40. Seasonal changes in the depth distribution of suitably-sized (3-18 mm long) *Macoma balthica* on the intertidal flats around Griend (from Piersma *et al.* 1993a). Note that in the explanatory cartoon (bottom panel) the surface of the sediment should have been drawn three layers higher.

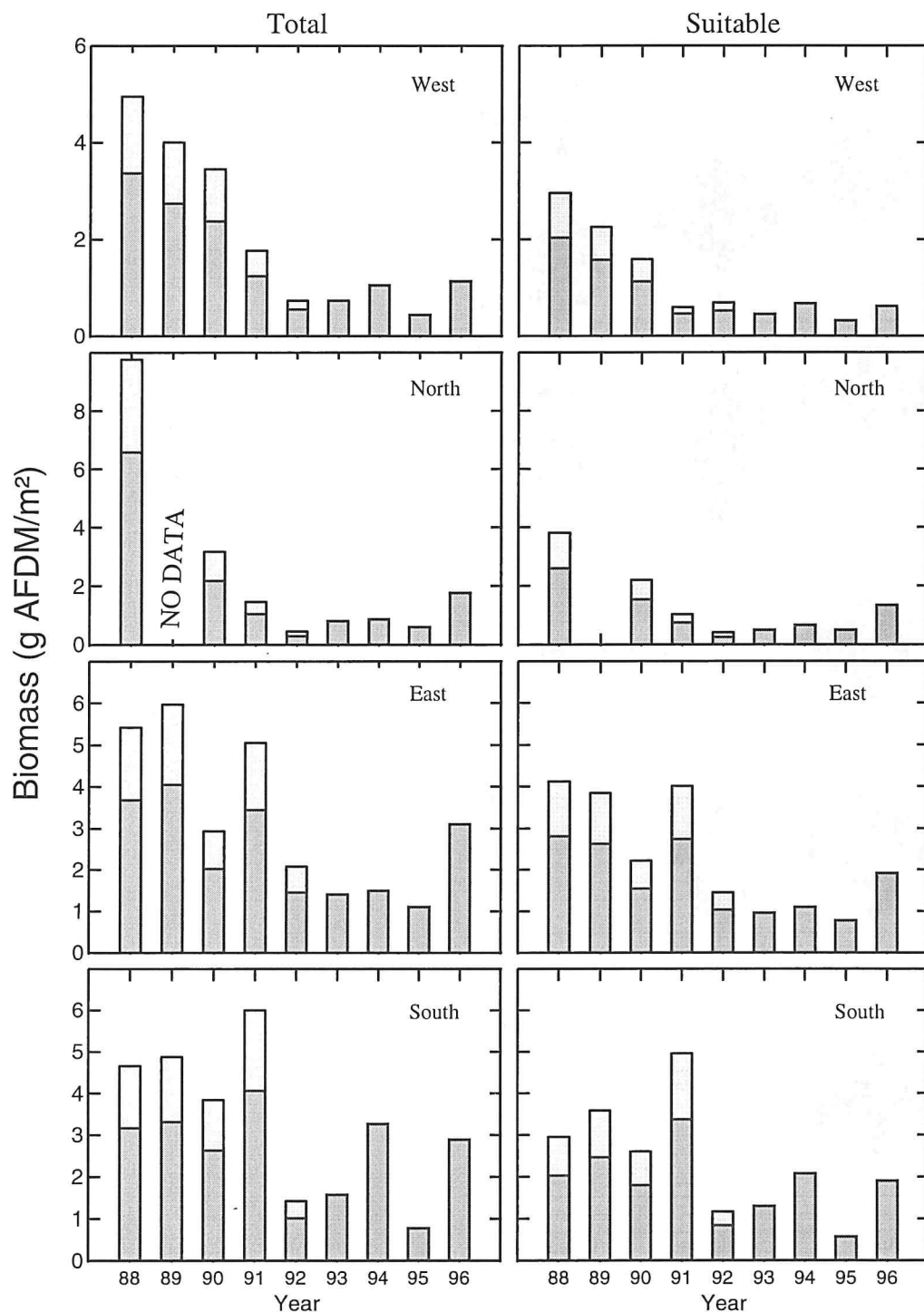


Fig. 41. Summary statistics (four panels with histograms) of the changes in biomass densities of *Macoma* in the different sectors around Griend in 1988-1996. Total biomass values are given at left, biomass densities of suitably sized *Macoma* at right. The unshaded part of the bars for 1988-1992 indicates the corrections for transect-sampling relative to the results of the grid-mapping approach (see Fig. 25).

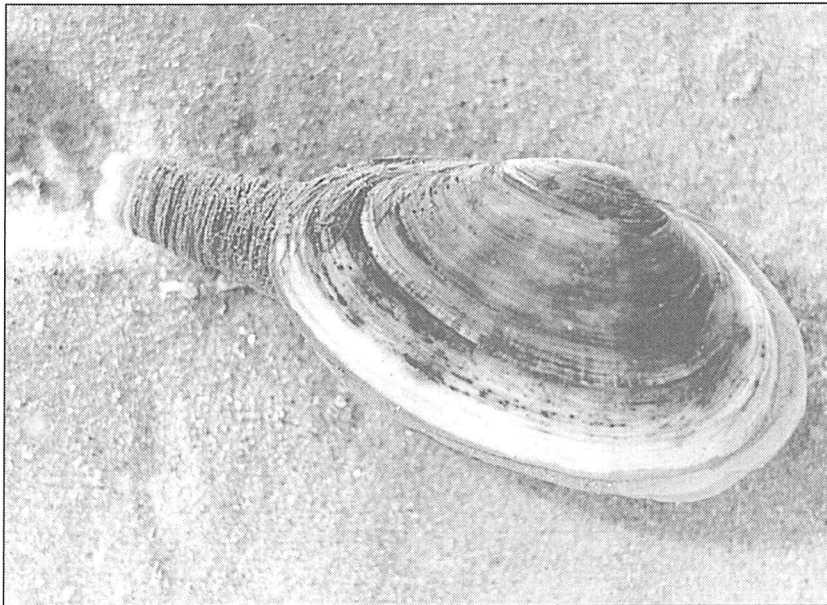


Fig. 42. Photograph of a Soft-shell Clam *Mya arenaria* with a half-extended siphon.
(photograph by Jan van de Kam)

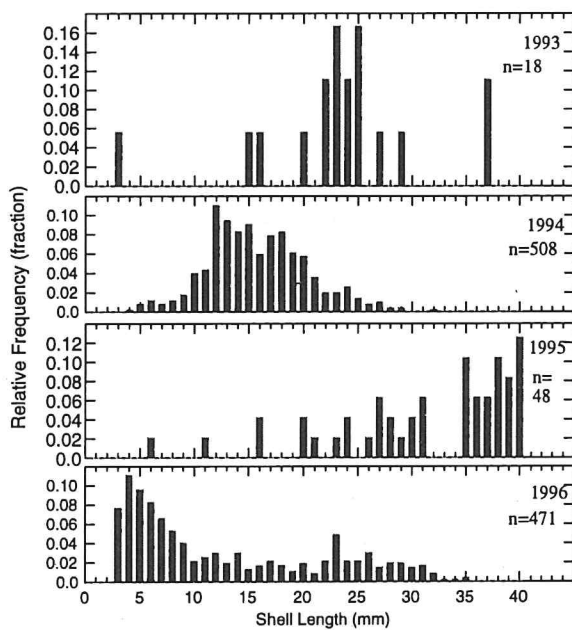


Fig. 44. Size distributions of *Mya arenaria* as determined in August-September on the intertidal flats around Griend 1993-1996. Maximum size is 40 mm (see caption of Fig. 43).

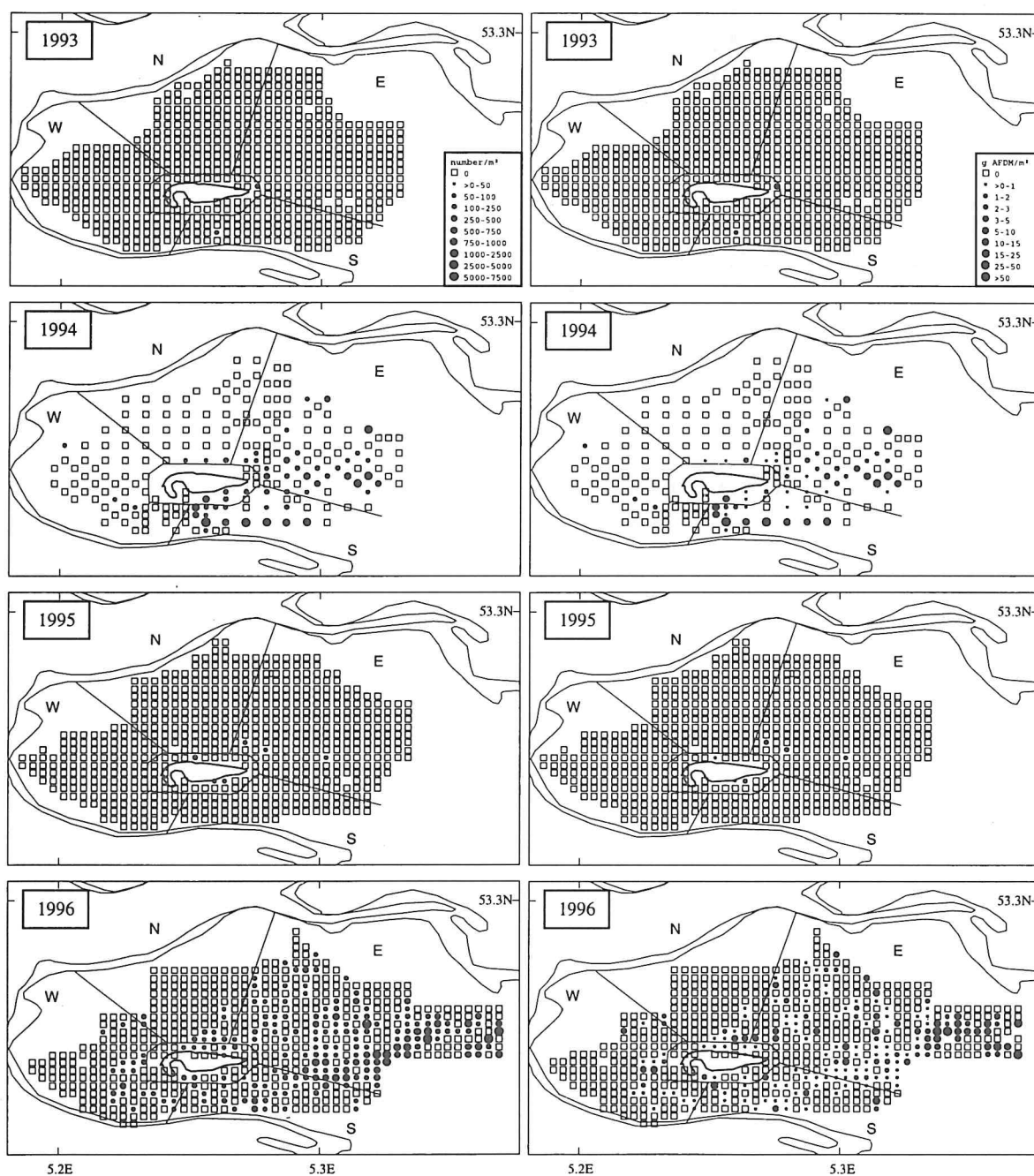


Fig. 45. Spatial variation in the densities (in numbers $[n/m^2]$, left) or biomass $[AFDM (g)/m^2]$, right) of suitably sized (ingestible: 3-20 mm long) *Mya arenaria* around Griend in 1993-1996.

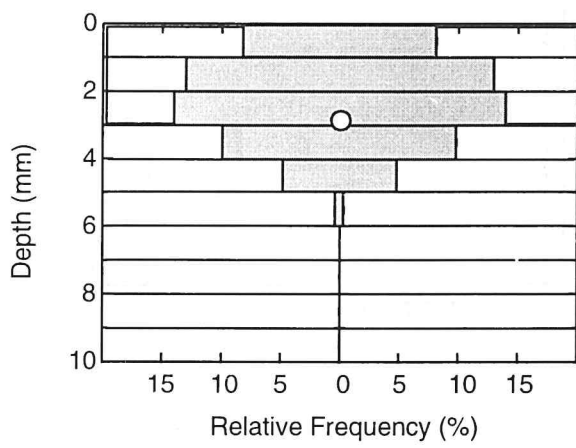


Fig. 46. Depth distribution of *Mya arenaria* in August 1994 ($n=151$).

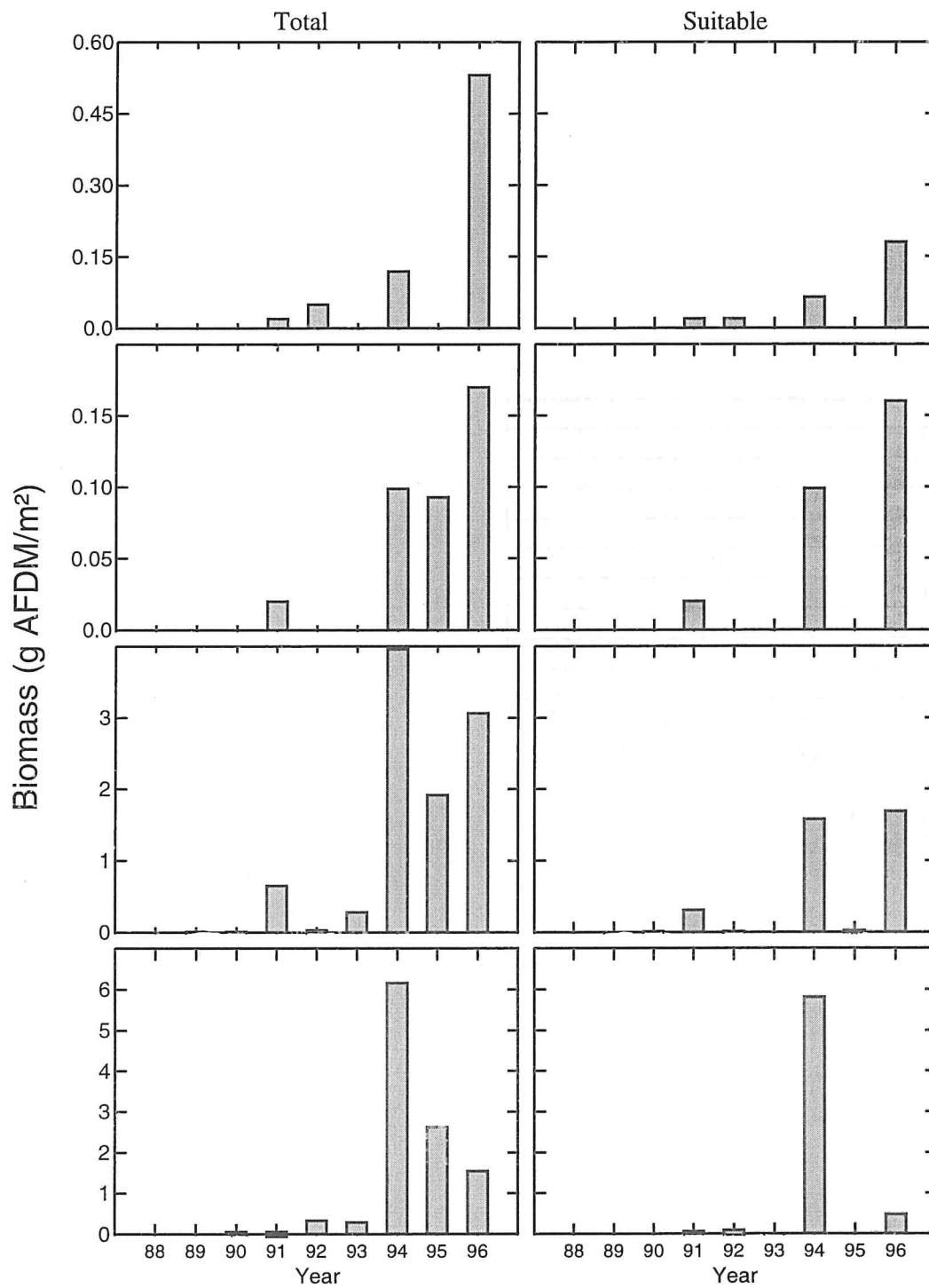


Fig. 47. Summary statistics (four panels with histograms) of the changes in biomass densities of *Mya* in the different sectors around Griend in 1988-1996. Total biomass values are given at left, biomass densities of suitably sized *Mya* at right. (Note that only *Mya* smaller than 40 mm are taken into account).

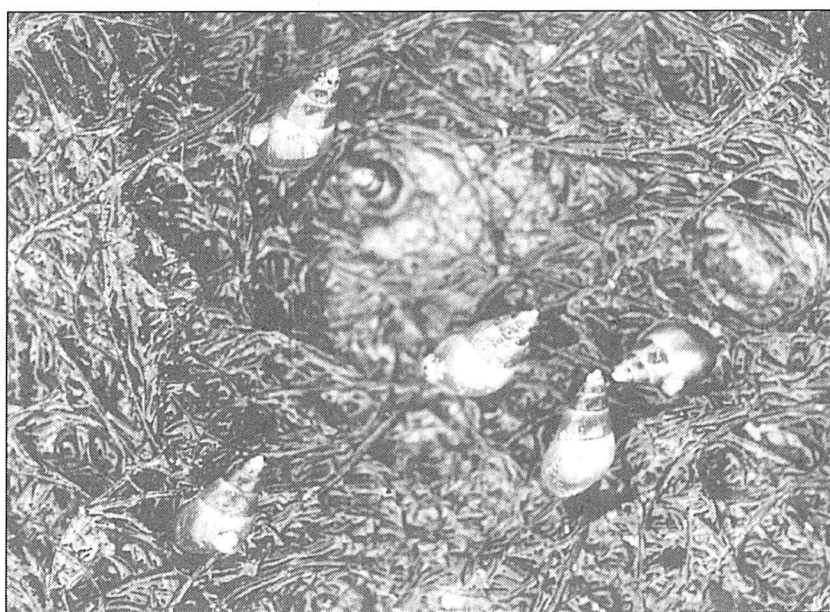


Fig. 48. A flock of Mudsnails *Hydrobia ulvae* crawling over bare sediment near a lugworm-cast (top panel) and a detail of a few Mudsnails on a patch of algae (bottom panel). (photograph by Jan van de Kam)

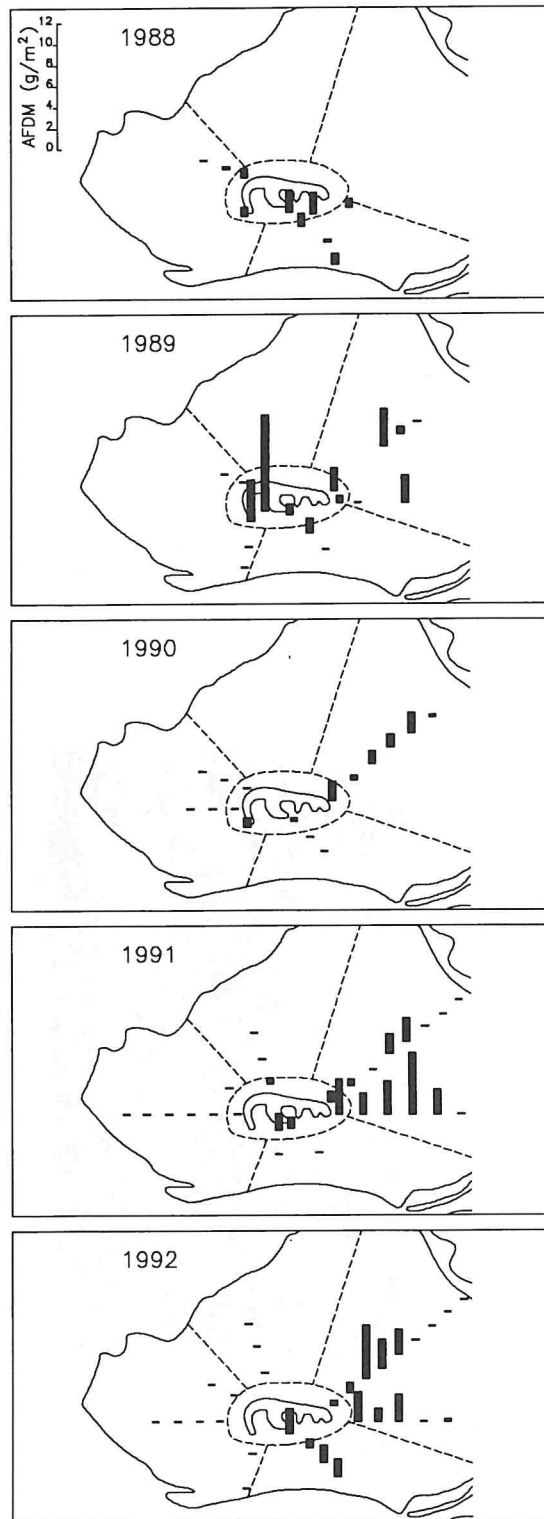


Fig. 49. Spatial and yearly variation in the overall abundance of *Hydrobia ulvae* near Griend in the period 1988-1992 (from Piersma *et al.* 1993a). At each sampling station 5 cores of 1/56 m² were taken.

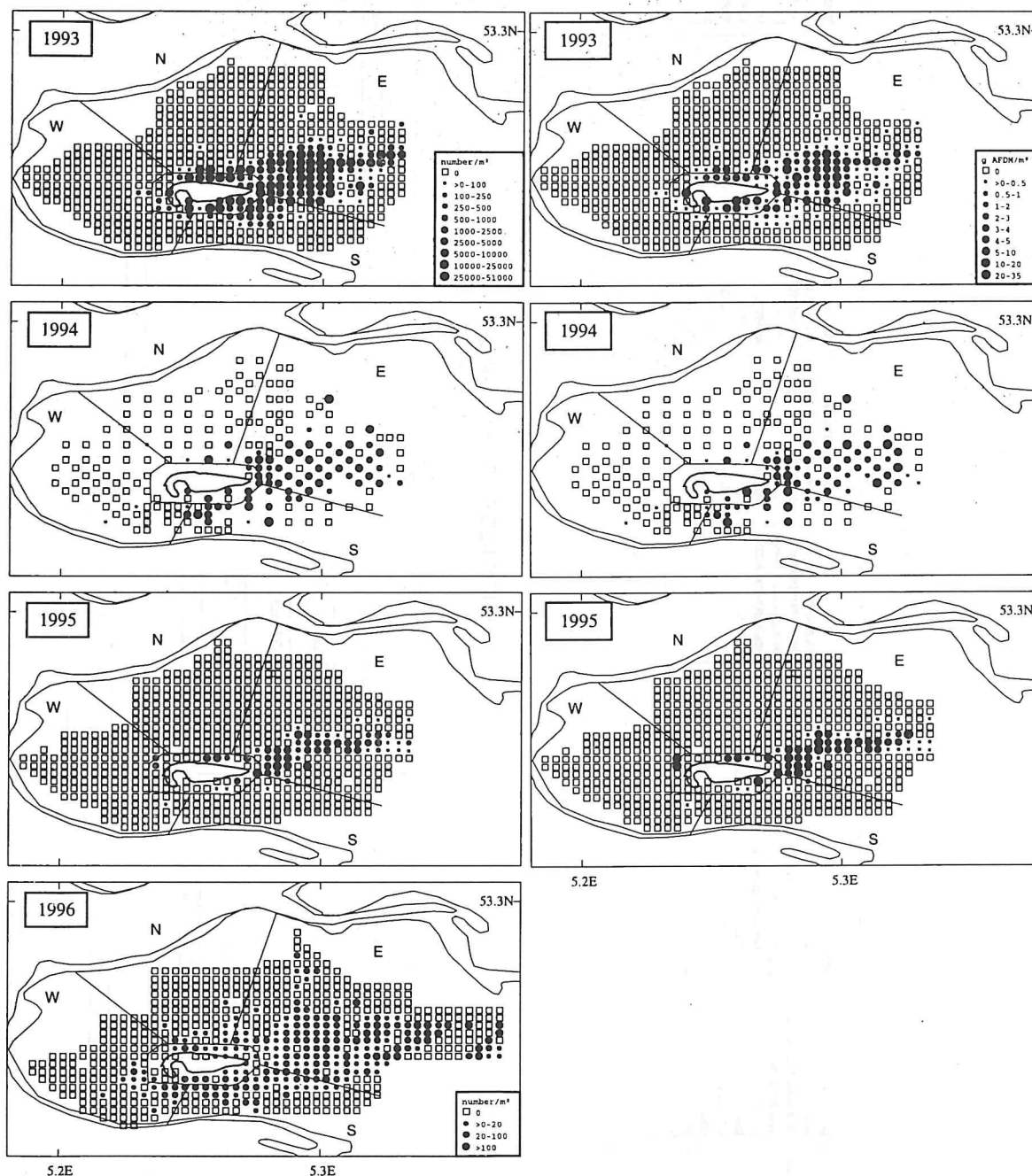


Fig. 50. Spatial variation in the total densities (in numbers [n/m^2 , left] or biomass [AFDM (g)/ m^2 , right]) of *Hydrobia ulvae* around Griend. Numerical densities are available for 1993-1996, although only in relative terms in the last year (necessary lab-work remains to be carried out at the time of report compilation); biomass densities are available for 1993-1995 only.

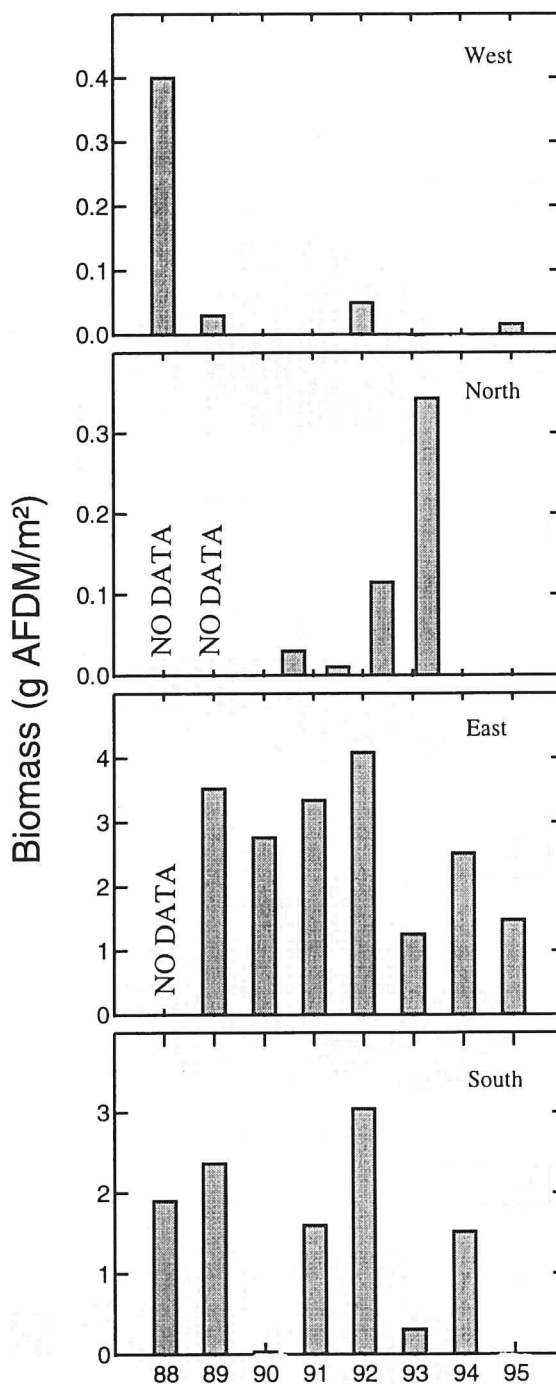
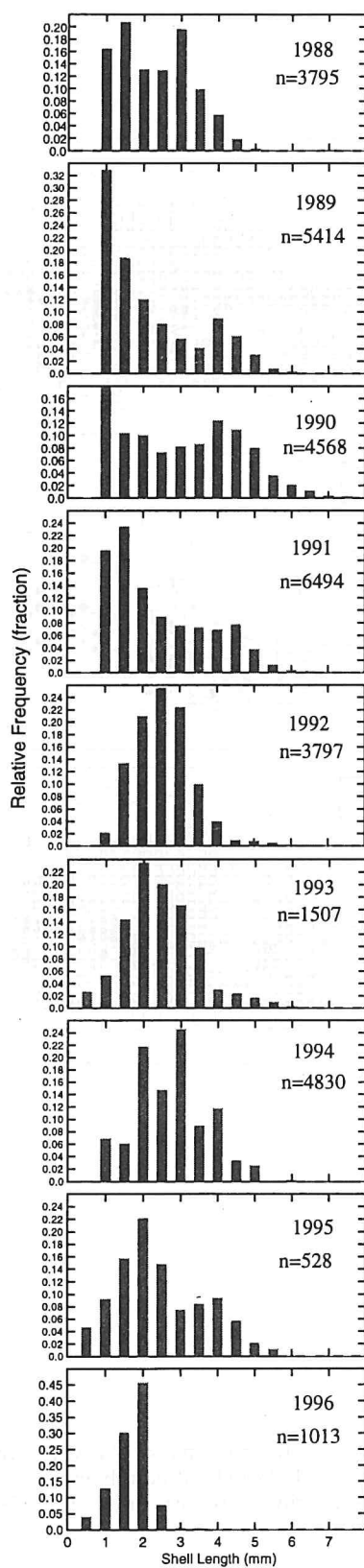


Fig. 52. Summary statistics (four panels with histograms) of the changes in biomass densities of *Hydrobia ulvae* in the different sectors around Griend in 1988-1995 (1996 data not available yet).↑

Fig. 51. Size distributions of *Hydrobia ulvae* as determined in August-September on the intertidal flats around Griend in 1988-1996.←

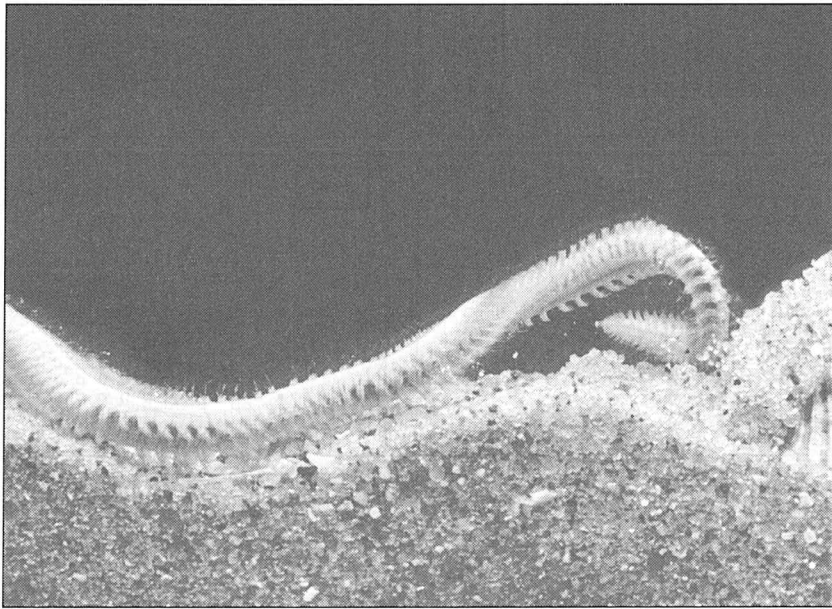


Fig. 53. Photograph of a Ragworm *Nereis diversicolor* crawling over the sediment. (photograph by Jan van de Kam)

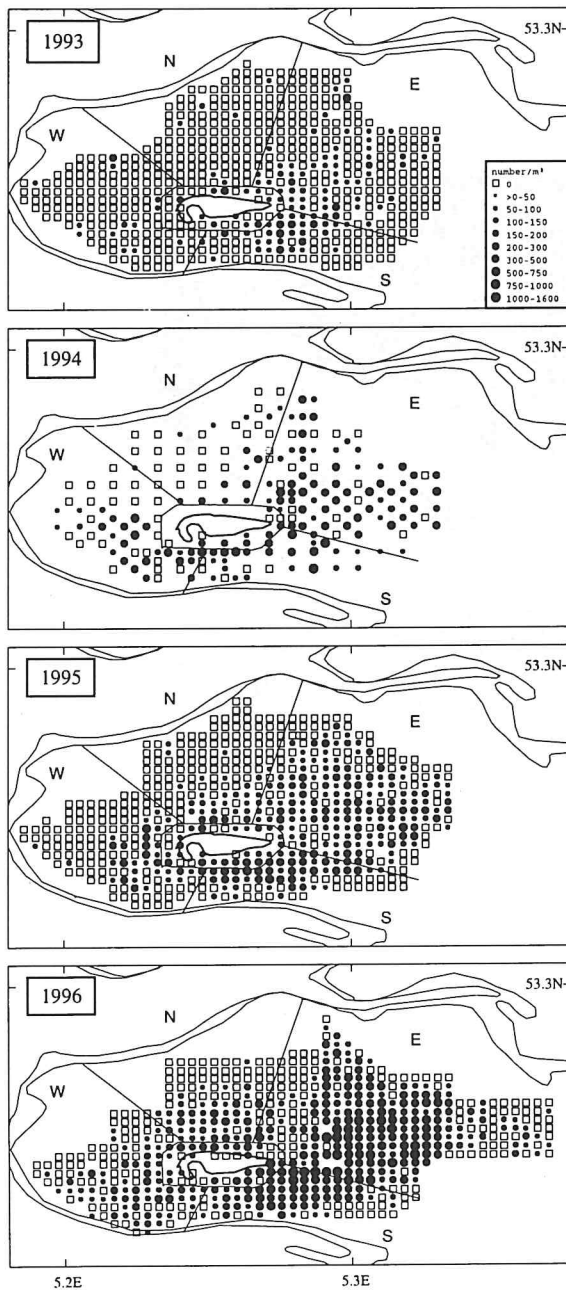


Fig. 54. Spatial variation in the total densities of *Nereis diversicolor*, the Ragworm, around Griend in 1993-1996.

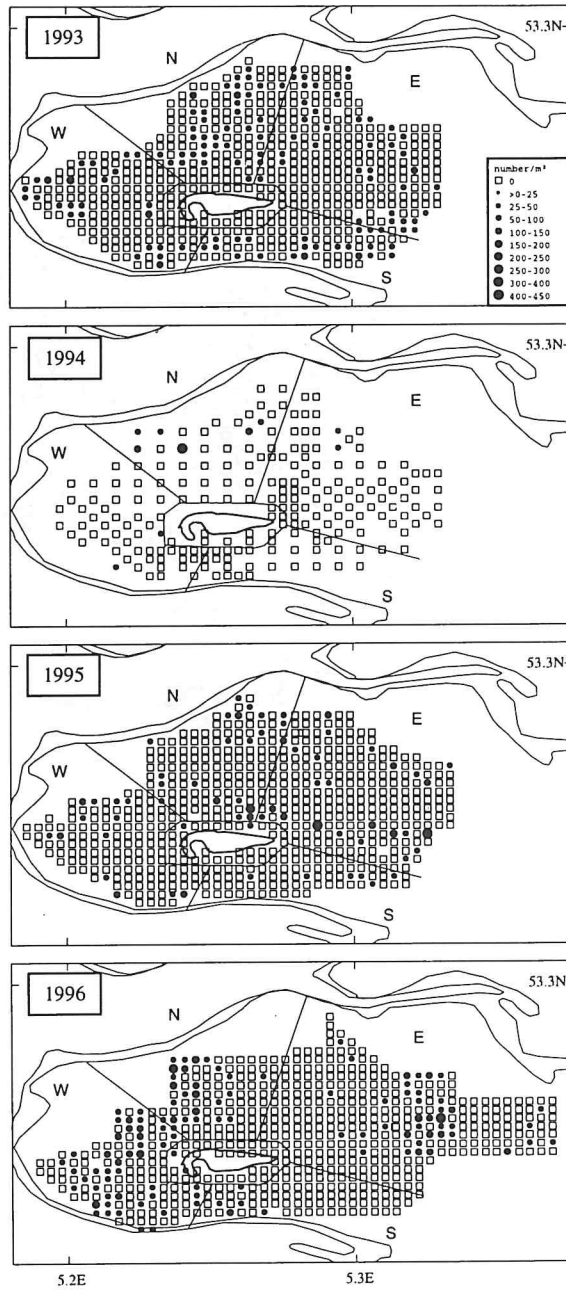


Fig. 55. Spatial variation in the total densities of *Nephtys hombergi*, the Catworm, around Griend in 1993-1996.

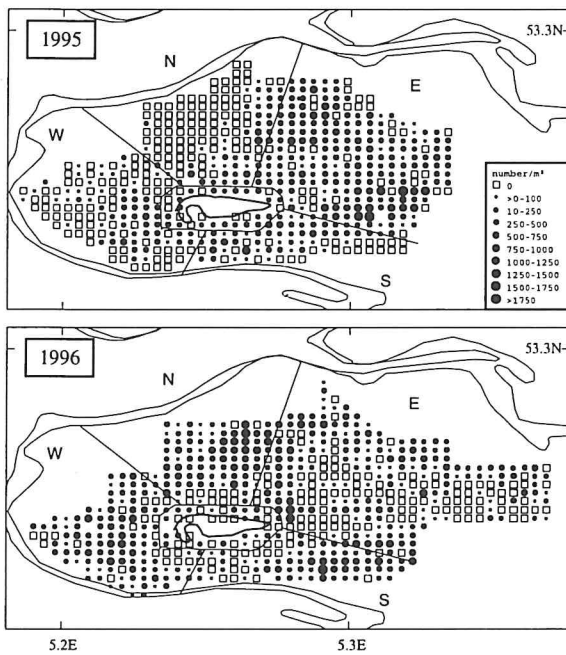


Fig. 56. Spatial variation in the total densities of the small polychaete *Scoloplos armiger*, around Griend in 1995-1996.



Fig. 58. Spatial variation in the total densities of the amphipod crustacean *Urothoe poseidonis* (Haustoriidae) around Griend in 1995-1996.

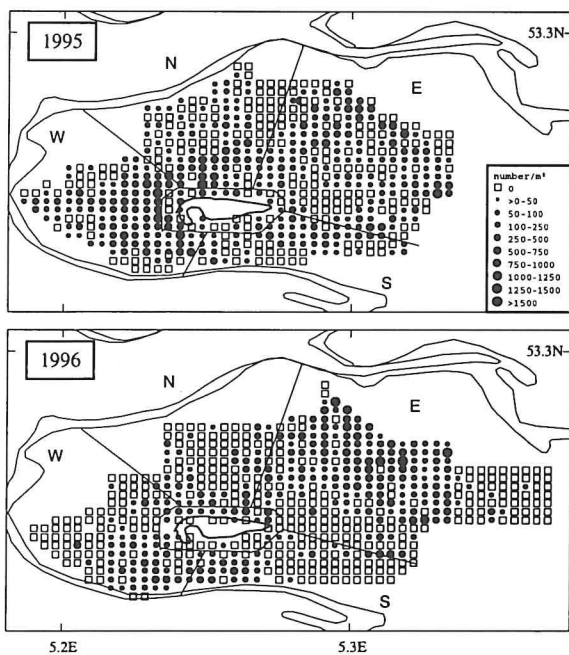


Fig. 57. Spatial variation in the total densities of the blood-red long polychaete worms of the Capitellidae family around Griend in 1993-1996

5. KNOTS

The focal bird species in this study, the Knot *Calidris canutus*, is a medium sized wader varying in body mass (depending on migratory state) between 120 and 240 g. Outside the breeding season they are greyish above and whitish below (Fig. 59). At other times they are much more colourful, with a rusty red breast and belly and a brownish-blackish back. Knots have a straight 3.5 cm long bill with which they probe in the sediment (Fig. 59). The tip of the bill is equipped with a big arsenal of sensory cells able to pick up the very subtle signals that betray hard objects (such as buried bivalves) in soft sediments when the bill tip is pushed into the top layer of the sediment (Piersma *et al.* MS1). Knots are very efficient in finding static objects in sandy substrates, and can thus occur in areas with relatively low standing stocks of small bivalves (Piersma *et al.* 1995). Knots may only be able to feed so efficiently in sorted sediments with particular grain-size and water content characteristics (Piersma *et al.* MS1).

The Knot is one of the more numerous coastal wader species using the East Atlantic Flyway (Piersma *et al.* 1987, Smit & Piersma 1989). One

reason for its relative abundance along the flyway encompassing the Wadden Sea is the occurrence of two subspecies (rather than one along most other flyways). In the nonbreeding season, large numbers of Knots of the *islandica* subspecies occur in the southern North Sea basin, including the Wadden Sea (Fig. 60). These *islandica*-Knots breed in high arctic Greenland and northeastern (high arctic) Canada (Davidson & Wilson 1992). Members of the Afro-siberian *canutus* subspecies occur in the Wadden Sea during northward (in May) and southward (in July-early September) migration. They winter in West Africa and breed in the west-central Siberian high arctic (Fig. 60; Piersma *et al.* 1992).

Knots traditionally are found in large numbers near Griend. On 16 August 1936 perhaps more than 10,000 birds were counted (Brouwer *et al.* 1950). Our first studies of the Knots in the Griend area have confirmed the likely presence of both *canutus* and *islandica* subspecies (Piersma *et al.* 1993a). The two subspecies both appeared to occur in reasonable numbers the first four years of study (1988-1991) but not in 1992, when hardly any Knots were recorded



Fig. 59. Portrait of a foraging Knot *Calidris canutus* in full winter plumage. Note the blurred picture of head and bill, indicating the technique of fast up and down movements of the head with a slightly opened bill probing the upper layer, which is used to detect static objects in the soft sediments. (photograph by Jan van de Kam)

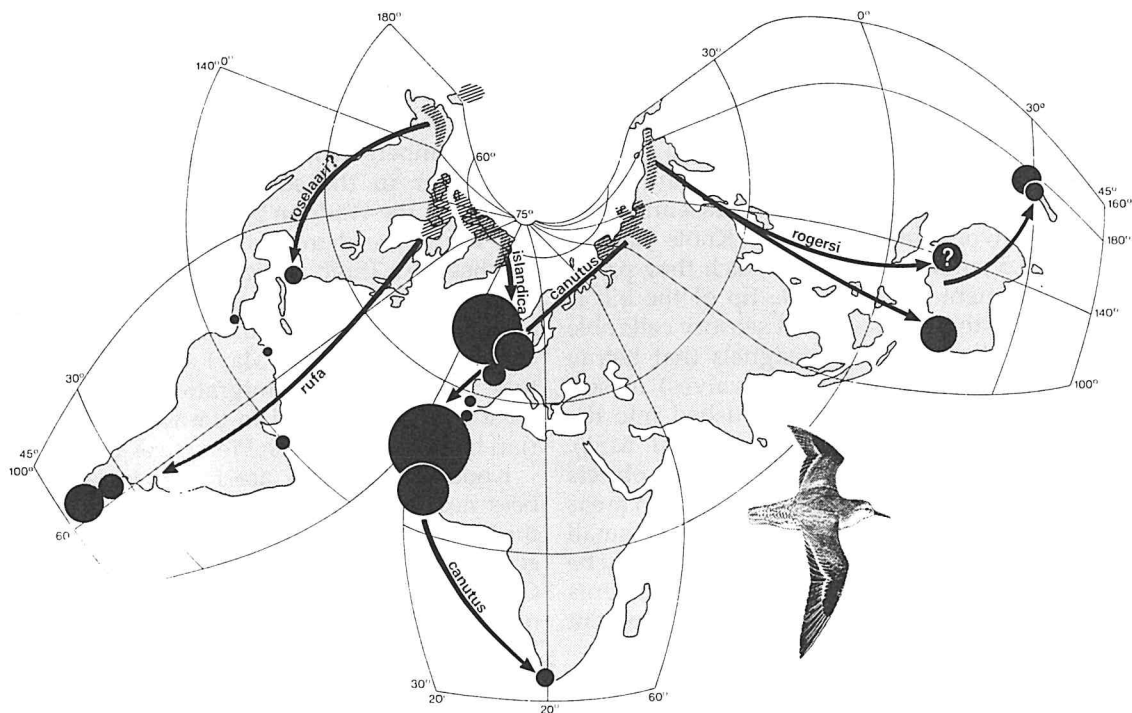


Fig. 60. Global distribution (area of circles indicating wintering numbers) and migration flyways of the various subspecies (indicated with the Latin names) of Knots. This figure was compiled from information in Piersma & Davidson (1992).

near Griend in periods that the particular subspecies should be present (Fig. 61; 22 July-11 August: *canutus*, 18 August-20 October: *islandica*). Although the data for *islandica* were somewhat fragmentary, it is clear that the absence of this category of Knots in 1992 is rather exceptional (a probability of 7.1%; Fig. 61 lower panel). The rather high number of *canutus*-Knots in 1991 and the virtual absence of *canutus*-Knots in 1992 also provide exceptional cases (with probabilities of 4.0%, lower than the accepted chance-level of 5%). Piersma *et al.* (1993a,c) argue that the low numbers of Knots near Griend in 1992 were due to the very low stocks of their favourite foods (see Zwarts & Blomert 1992), particularly *Macoma balthica*. As we have seen above, some alternative food species have been available in the years since 1992, and the question is thus whether and how the Knots responded, both with respect to their numbers and area-use, as with respect to their diet choice.

5.1. Methods

Numbers

Since 1964 the wardens of Griend carried out high-water counts of all waterbirds roosting on and close to Griend at approximately weekly intervals in the period April-July. Outside the breeding season, supplementary counts were made by visiting parties at irregular intervals. The data collected between 1964 and 1987 have been summarised by Veen & van de Kam (1988), and an updated data series has been analysed for Knots by Piersma *et al.* (1993a; and see Fig. 61). Before 1988 Knots regularly roosted in the saltmarsh area of Griend, very close to the warden's house (Fig. 62). Since then, this habit appears to have been given up, and we only very rarely encountered Knots in the saltmarsh area, usually in early August, a period when *canutus*-Knots should have been around.

Weather, logistics and volunteer effort permitting, Knots were intensively studied every year

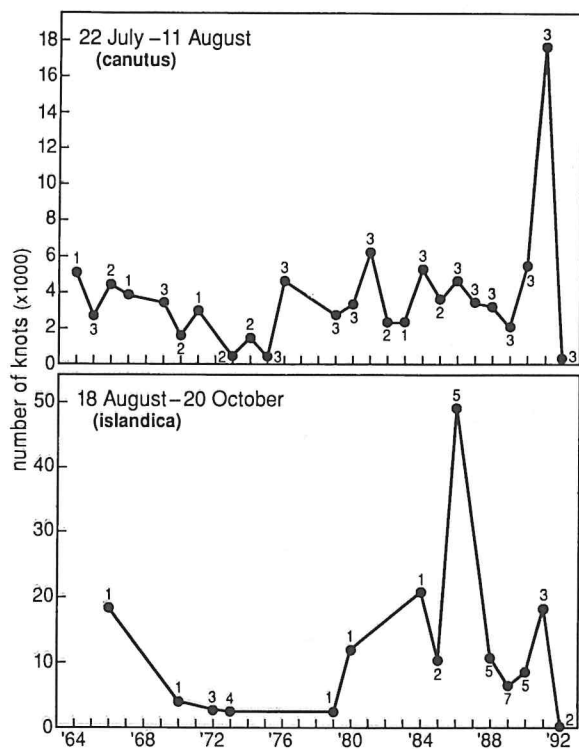


Fig. 61. Long-term changes in the average numbers of Knots occurring near Griend in late July-early August (*canutus* subspecies) and late August through October (*islandica* subspecies) in 1964-1992 (from Piersma *et al.* 1993a).

(1988-1996) in the period August-October. Before 1988, when the island was small, the whole area exposed at high tide could usually be surveyed from the warden's house (Fig. 63). This became impossible with the construction of the 2.5-km long dike, behind which much of the area and many roosting flocks disappeared from sight. Since then, Knots (and other waterbirds) have been counted by two parties of 1-2 persons, one covering the west end and the other the eastern half of the island.

At the start of the study in 1988, it became clear that at the higher high tides a lot of birds disappeared from Griend during high water, having first assembled on the high-lying flats northeast of Griend and then flying to Richel. Since this discovery, most counting parties took the effort to separately count any Knots flying to Richel, but there is some inconsistency in the methods here. We do not know whether the roost flights to Richel are a recent phenomenon

coinciding with the building of the large dike or changes in the topography of Richel, or whether Knots and other shorebird species also routinely flew onto Richel before 1988.

Foraging distribution

Movements to and from Richel to the feeding areas around Griend were monitored as often as possible and the approximate flight trajectories pencilled on a map. In study periods on the island, we went out on the intertidal flats during most low-water periods. We recorded the approximate time in the field and noted the area checked for the presence of Knot flocks on maps along with a description of observer movements. The positions and sizes of encountered Knot flocks were also recorded on the map, based on triangulation of compass-bearings taken in the field (usually on the lighthouse in West-Terschelling, the beacon on Griend and the highest church-tower in Harlingen), and more recently using handheld GPS. Also, flight paths of recorded flocks and the timing of movements were recorded on maps of the area. The daily map-recordings served as the basis for the description of area-use and movements of Knots over the study area. To avoid biases in the estimates of area-use due to unequal area cover during observation trips, we only included observations of flocks made in any one of the four sectors around the island (of fairly similar surface area) indicated in fig. 2 of Piersma *et al.* (1993a, p. 333), and for which we know that the timed visit per observation day was close to the average length (3-5 hrs).

Diet

The diet of Knots was described by the analyses of large numbers of dropping samples using the methods outlined in detail by Dekinga & Piersma (1993). Briefly, counted numbers of droppings were collected on the intertidal feeding areas at regular intervals. We collected them either with a spoon or with a valve of a large bivalve. Droppings were usually stored frozen, then dried at 55-60°C to constant mass, and sieved over a 0.3 mm mesh. The shell mass retained on this sieve is used to estimate the total shell mass in the faeces (equations in Dekinga & Piersma 1993). Sieved shell fragments were sorted to species and the species' contributions weighed. The total length of partially broken *Hydrobia* shells, and the height of intact



Fig. 62. A flock of Knots roosting in open patches within the saltmarsh area of Griend in the early 1970s. (photograph by Jan van de Kam)

hinges of *Macoma*, *Cerastoderma* and *Mya*, were measured under a binocular microscope with an ocular micrometer. Observer-specific regressions of hinge height on shell length were fitted to estimate the size distribution of ingested molluscs (see Dekinga & Piersma 1993). The compositional analyses of shell and meat in terms of ash, dry mass and AFDM, described above, yielded the site- and time-specific ratios to translate the species-specific shell masses into the contributions in biomass terms of the different mollusc species to the diet of Knots (see Appendix of Piersma *et al.* 1993a). Although

these detailed analyses allowed an exact determination of diet composition, we usually tried to back up, by visual observations of prey choice in the field, our findings based on drop-pings.

5.2. Results

Numbers

Up to 1996, numbers of Knots have never again been as low as in 1992 (Fig. 64). Although Knots were not very numerous in 1993 either, substan-



Fig. 63. Before 1987, when the island of Griend was small and not yet reinforced by a dike, it was very straightforward to count the waterbirds at high tide: they all congregated close to the warden's house. This is nicely illustrated by this flock of waders alighting close to this house/hut on poles. (photograph by Jan van de Kam)

tial numbers were seen in 1994 (especially in the early period when *canutus* should have been around) and rather late during the season in 1996. In both years numbers of Knots in the neighbourhood of Griend were rather higher than the long-term overall average of 7300 Knots, at least part of the time (Fig. 64), and in both years Knots capitalised on an interesting alternative prey to *Macoma*, abundant spat of the Soft-shell Clam *Mya arenaria* (see below).

Diet

In the first two years of this study (1988-1989), when Knots were foraging in quite large numbers on the intertidal flats near Griend (see Piersma *et al.* 1993a,c and Fig. 66), they fed predominantly on *Macoma* and *Hydrobia* (Fig. 65). *Macoma* was taken early in the season and *Hydrobia* later on, at a time when *Macoma* retreated deep in the substrate (see Fig. 40). Even though some suitably sized *Cerastoderma* were around (albeit in rather small quantities, see Fig. 31), the

latter prey, one with a heavy shell, was obviously avoided, and the Knots near Griend thus obeyed the diet-predictions of Zwarts & Blomert (1992). However, over the subsequent four years *Cerastoderma* dominated the diet, with *Hydrobia* being second most important (Fig. 65). In these years larger numbers of suitably-sized *Cerastoderma* were around than in 1988-1989, but the rather lower numbers of Knots capitalising on them (especially in 1992), suggested that they were rather second choice. This became especially clear in 1994 when suitably-sized *Cerastoderma* was around in densities comparable with the previous four years (Fig. 31), but when two attractive alternative prey *Mya* and *Mytilus* were also available. Accordingly, the diet of Knots consisted for a very large part of these two prey (Fig. 65). In 1995 *Hydrobia* and *Macoma* again contributed a great deal, and in 1996 the Knots, once more capitalised on the available small *Mya*, with the then rather numerous *Cerastoderma* also commonly consumed.

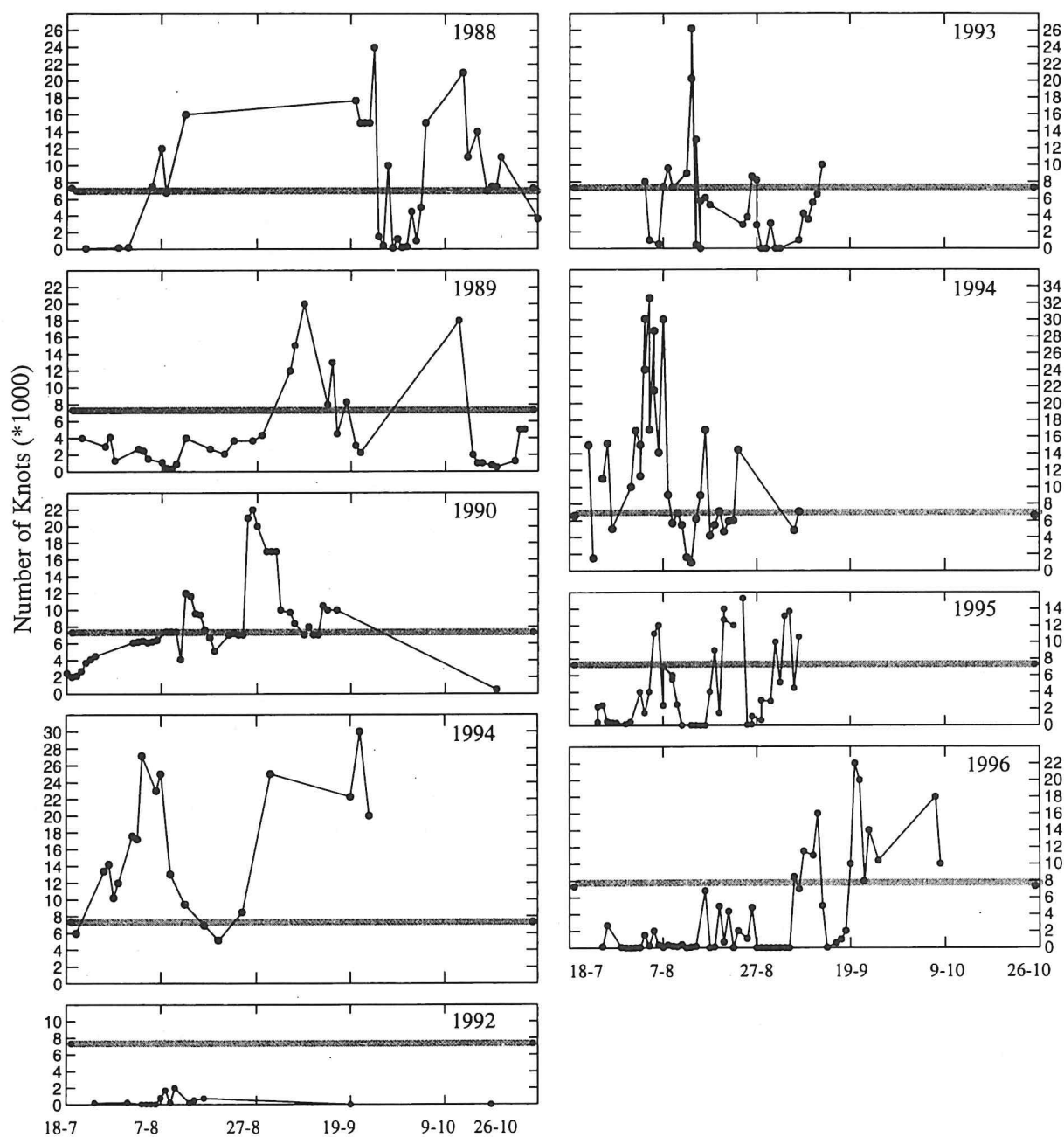


Fig. 64. Numbers of Knots observed roosting on Griend including, in cases where this was observed, the numbers flying on to Richel, in July-October 1988-1996. The horizontal shading indicates the overall average number of Knots.

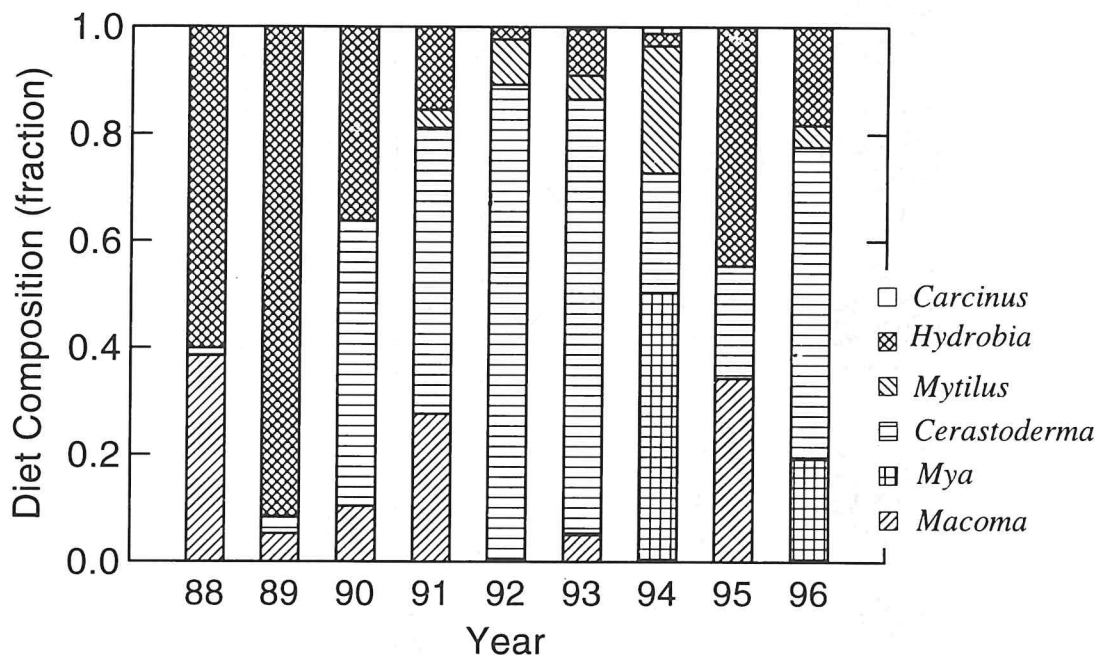


Fig. 65. Changes in the diet in August-September, expressed as contribution to the ingested biomass (see Dekkinga & Piersma 1993), of Knots around Griend. This figure is based on the following sample sizes in the different years (number of dropping samples, followed by the total number of individual droopings within these samples): 1988: 25, 2450; 1989: 1, 39; 1990: 10, 950; 1991: 17, 1253; 1992: 8, 500; 1993: 28, 1476; 1994: 39, 1862; 1995: 18, 1896; 1996: 18, 994.

Foraging distribution

In 1988, Knots intensely used the northern and eastern sector (Fig. 66), but in the years thereafter virtually abandoned the northern sector. They have returned a few times from 1993 onwards, but by and large the northern sector has been abandoned since 1988. The use of the western sector has declined slowly, but has been low throughout. The use of the eastern sector has also consistently decreased. Only the southern sector, the region least affected by the shell fisheries, has shown a rise in usage, but no Knots were observed there in 1996 (Fig. 66).

Even though there is no clear trend in the numbers of Knots passing Griend for Richel with the incoming tide or roosting on Griend

(Fig. 64), the overall numbers feeding on the intertidal flats surrounding the islands do show a clear decline since 1988, the first year of observation (Fig. 67; note that the numbers of Knots in the Griend area were not particularly high in 1988, see Fig. 61). Only in 1996, a year for which we also have reported some kind of return to original substrates and rather good stocks of benthic bivalves suitable as foods (Chapters 3 and 4), there is a sign that this trend stops or shows a reversal. Even so, in 1996 the numbers of Knots using the Grienderwaard to feed were still at only 40% of their former level, after having been reduced to 5-40% in the intervening seven years.

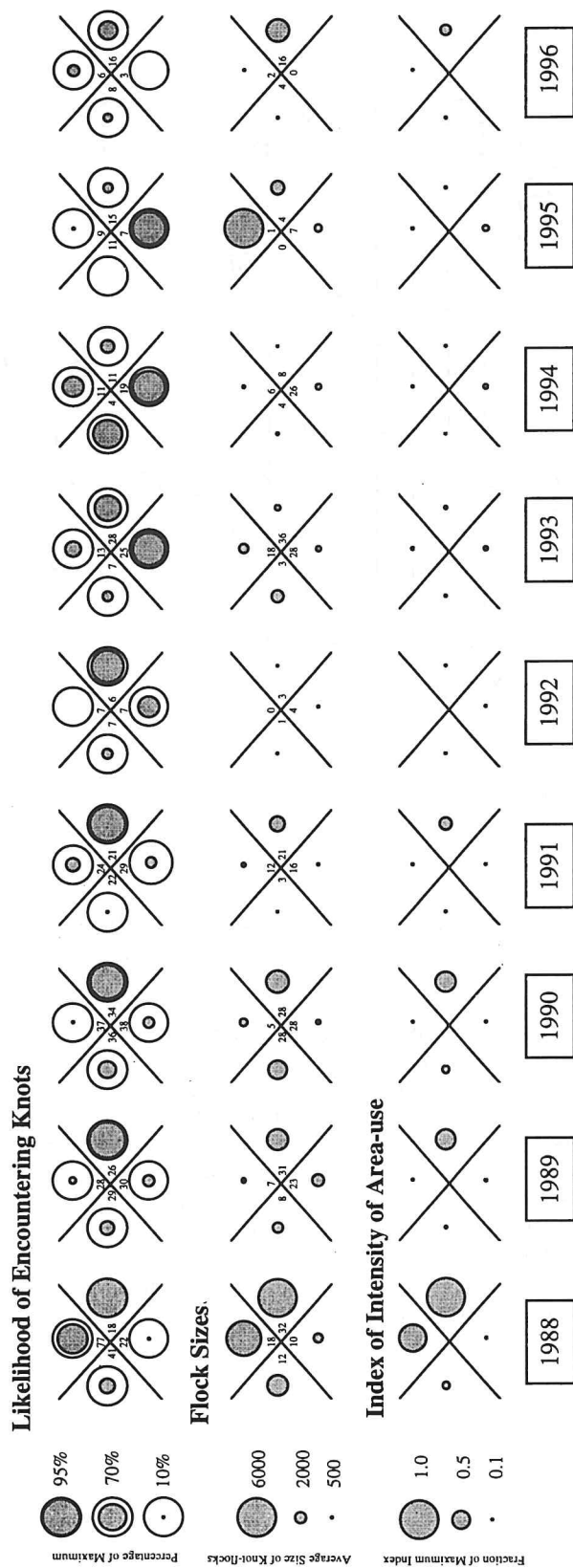


Fig. 66. Changes in the incidence of Knots foraging on the different sectors (see fig. 2 in Piersma *et al.* 1993a) of the intertidal area around Griend in 1988-1996. The 'index of area-use' is calculated by multiplying the fraction of occasions that flocks of Knots were observed in a sector when this sector was actually visited, times the average numerical size of the flocks seen in this sector. The little numbers near the centre of the cross indicate the number of times a sector was searched for Knots (top row) and the number of counted Knot-flocks on which average flock-size was based (mid row).

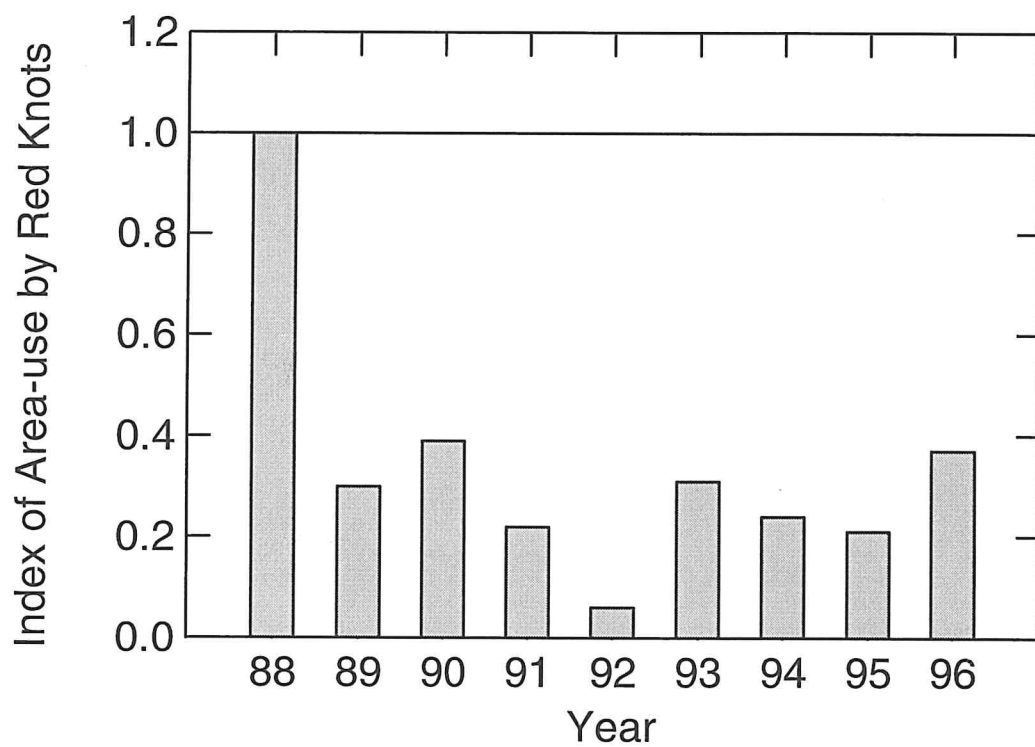


Fig. 67. Changes in the numbers of Knots using the intertidal flats around Griend (Grienderwaard; index of intensity of area-use) to feed, expressed as an index with the 1988-figure set at 1.0. See caption to Fig. 66 for additional information.

6. WHAT HAS HAPPENED AROUND GRIEND IN 1988-1996?

In the foregoing chapters we have described, for the period of study 1988-1996, the gross geomorphological changes of the island of Griend and its surrounding intertidal flats as a consequence of human economic and conservation activities (Chapter 2), the changes in sediment characteristics (especially with respect to grain-size parameters) and the possible reasons for these changes (Chapter 3), the long-term changes in the stocks of various macrobenthic animals, part of which may be used as food by the focal shorebird species, the Knot (Chapter 4), and the changes in overall numbers, diet choice and differential area-use of Knots on the intertidal flats around Griend (Chapter 5). Here, we will try to bring the various findings into causal context, relying on historical studies made in the western Wadden Sea, and on topical studies of comparable processes carried out elsewhere in the world.

6.1. An insightful large-scale historical experiment

Our sedimentological studies have shown that on the intertidal flats around Griend the biggest change in sediment characteristics (a loss of silt and an increase in the median size of the remaining particles) occurred in the western and northern sectors. In the eastern sector the change was rather small and in the southern sector there was even a change to somewhat siltier sediments. We have argued in Chapter 3 that it is no coincidence that losses of silt, and increases in grain-size, should have occurred in the sectors that have witnessed heavy mechanical cockle dredging (northern sector) and the removal of protective mussel banks (especially the western sector), whereas the southern sector might have benefitted from the increased lee-effect of Griend becoming a much larger island. Together with the changes in sediment characteristics, the benthic bivalve populations either showed large decreases (in the western and northern sectors), marginal decreases (in the eastern sector) or small increases in abundance (southern sector). In turn, these changes in food availability for Knots are perfectly correlated with their use of the different sectors. Knots

have kept away from much of the western and northern sectors after 1988 and increased their use of the southern sector. Given the usual limitations of historical studies such as this one, fate nevertheless provided us with quite a nice experimental set-up. There were shellfisheries in two sectors, there was one control and one sector with a contrasting treatment: the provision of lee). The remaining problem is that treatments were not replicated (cf. Thrush *et al.* 1995). But were they really not?

The long-term studies of Beukema and associates, carried out in the westernmost portion of intertidal flats of the Wadden Sea, Balgzand (Beukema *et al.* 1978, Beukema 1989, 1991, 1992), in fact provides us with this replicate. Balgzand is located east of, and thus in the lee of, the dikes protecting the province of Noord-Holland. The area is thus much less wind-affected by (south- and north-) westerly storms than substantial parts of the western Wadden Sea. Although even at Balgzand all mussels were carted off in the frenzy of 1990 (Beukema 1993b), this area has been less exposed to cockle-dredging than many other areas of the Wadden Sea (J.J. Beukema & R. Dekker pers. comm.), although some mechanical harvesting of Lugworms *Arenicola marina* takes place (Beukema 1995). Under the hypothesis that shellfisheries in various ways destabilise sediments and induce the loss of silt and small sized sandgrains, particularly if dredging takes place during stormy periods, that in turn reduce recruitment of bivalves (Fig. 17, and see below), we predict that at Balgzand the populations of bivalves show recovery after the losses in 1990-1991. In fact, this is exactly what the data show us. In contrast to Griend, stocks of Edible Cockles at Balgzand (Fig. 68) rebounded after a serious dip in 1991. The sharp decline since 1994 does not change the overall picture that, contrary to Griend, at Balgzand Edible Cockles showed the ability to recover. For Baltic Tellins the patterns are even more convincing (Fig. 69). Where stocks dropped and did not recover around Griend, at Balgzand *Macoma* quickly recovered from the additional predation-induced mortality in the winter of 1990-1991. The observations are thus consistent with the 'negative biodepository spiral'-model (Fig. 17). Actually, the predictions are held up

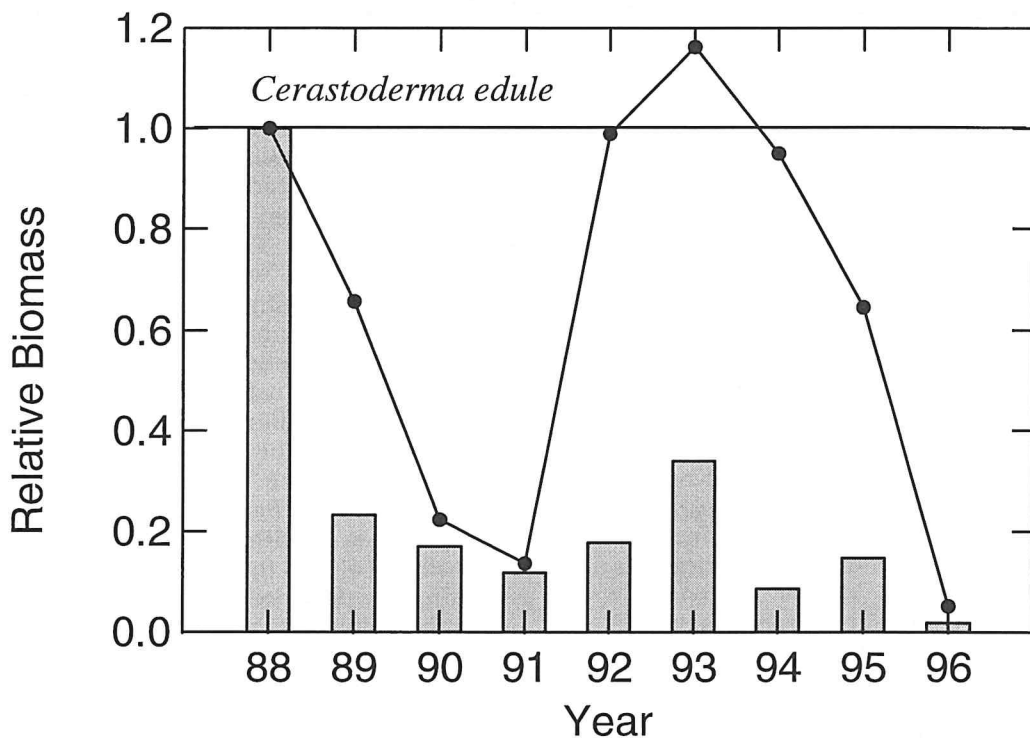


Fig. 68. Comparison of the long-term changes in total biomass of *Cerastoderma edule* around Griend (histogram) and at Balgzand (line graph; these data were kindly provided by W. de Bruin, J.J. Beukema and R. Dekker). Contrary to Griend, Balgzand shows a temporary recovery after the fishery pressure in 1988-1990.

even in a within-Balgzand comparison. Over the last five years, *Cerastoderma* and *Macoma* populations have shown decreases in the sandiest areas, and kept constant or showed slight increases in the muddier areas (R. Dekker & W. de Bruin pers. comm.).

The consistency with which the 'negative biodepository spiral'-hypothesis can explain all the variation in the documented changes of the abundance of benthic bivalve populations, in fact refutes other explanations sometimes put forward in the popular press. These include references to recent reductions of nutrient loads in coastal waters (perhaps signaling the end of an era of eutrophication) affecting algal growth and hence shellfish food availability and production, and the possible occurrence of large-scale poisoning incidents (see Smits 1997, Boddeke 1997). Under these hypotheses one would predict shellfish stocks to decrease without any correlations with (changes in) sedimentological conditions. As it turns out, even though eutrophication is still with us, densities of

Macoma at exposed sandy areas at Balgzand have never been as low as they are at present (R. Dekker pers. comm.). In 1997 *Macoma* stocks in the exposed parts had reached levels lower than those in the early 1970s, at a time when despite lowering phosphate values, decreases of algal abundance and primary production had not yet occurred (Cadée & Hegeman 1991, 1993 Cadée 1992, pers. comm.), and in spite of the favourable climatic conditions for recruitment that occurred over the preceding two winters.

6.2. Sediments, hydrodynamics, fisheries and shellfish populations

There are three issues to be addressed now: (1) what is known about immediate effects of trawling or dredging on sediment characteristics, including increases in boundary layer water-current velocities, with the loss of structures such as mussel banks, and also in relation to normal environmental stresses such as

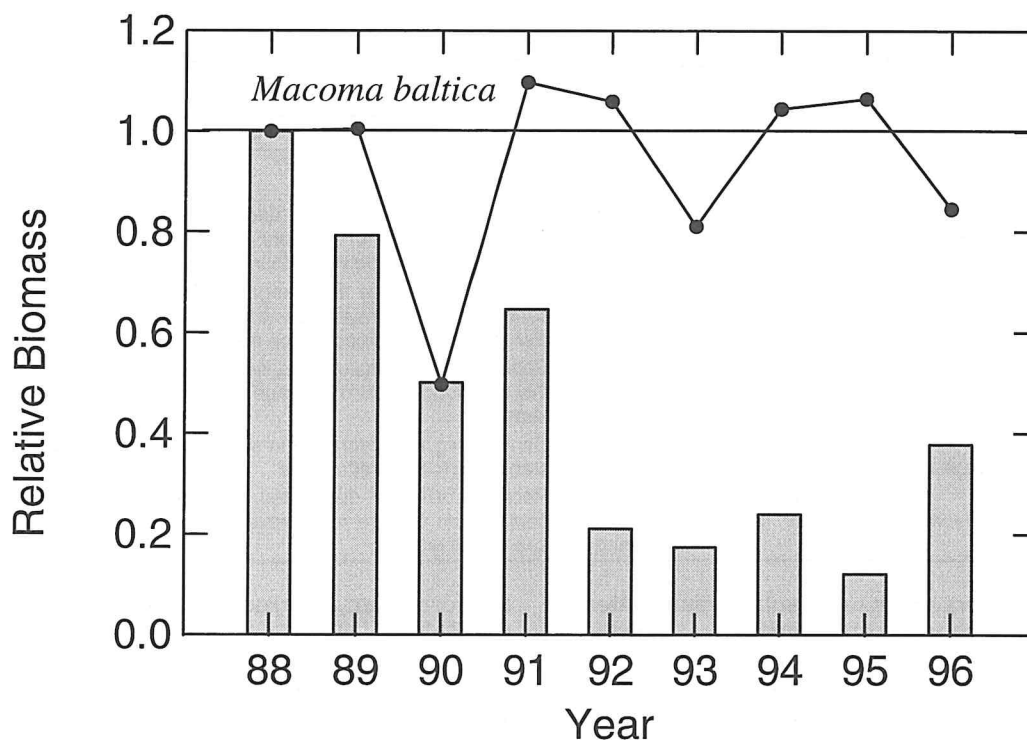


Fig. 69. Comparison of the long-term changes in total biomass of *Macoma balthica* around Griend (histogram) and at Balgzand (line graph; data kindly provided by W. de Bruin, J.J. Beukema and R. Dekker). Contrary to Griend, Balgzand shows a recovery after the fishery pressure in 1988-1990.

storms, (2) what is the role of the benthic bivalves themselves in maintaining particular kinds of sedimentary habitats, and (3), could changes in sediment characteristics influence the settlement of spat?

Sometimes, when critical substrates are simply knocked off in the search for an economically valuable shellfish resource (Fanelli *et al.* 1994, Table 1), the fishery-effects on the abiotic environment are perfectly clear. As is not unusual in comparisons with rocky shore ecosystems, the effects of trawling, digging and dredging on substrate characteristics and animal communities of soft sediments are harder to see and to study, and may occur more 'thinly spread' over larger spatial scales, than on the rocks (cf. Table 1, and see Hall *et al.* 1990, Hall & Harding 1996). Nevertheless, in his recent review of physical disturbance and marine benthic communities, Hall (1994, p.194) states that "there is increasing recognition of the rôle man plays in physically disturbing marine sediment environments, the most obvious and wide-

spread being commercial fishing" (and see Dayton *et al.* 1995, Roberts 1997). In spite of the scanty data on the subject, the removal of quite robust vertical structures such as mature mussel banks (Fig. 70) increases tidal prism, which leads to stronger currents and thus to the loss of particular grain-size fractions of the upper sedimentary layer (this report). It can safely be argued that the destruction of mussel banks makes an area ready for storm damage, which in turn may make re-invasion of denuded sand-flat areas by mussels (and many other bivalves) more difficult. In a study on the effects of storms on the distribution of mussel banks in the Wadden Sea of Schleswig-Holstein, Nehls & Thiel (1993) concluded that the longest-living mussel banks occurred in areas where there is some degree of shelter, where the banks get some degree of protection from westerly storms. In more general terms, wind and tidal stress factors seem to influence benthic community structures quite strongly (e.g. Warwick & Uncles 1980, Thistle 1981, Emerson 1989).

TABLE 1

Some examples of studies documenting consequences for sediment characteristics of perturbations made by humans in search for harvestable marine biological resources.

Biological resource	Area	Type of fishery	Effects on sediments and biota	Authority
Bottom fishes	offshore NE USA	Trawling	Sediment resuspension and loss of muds from fished areas	Churchill 1989
Hard Clam <i>Mercenaria mercenaria</i>	North Carolina	Clam 'kicking'	Sediments are reworked and made more 'dynamic'; no recovery of sea- grass beds within period of four years	Peterson <i>et al.</i> 1987
Scallop <i>Placopecten magellanicus</i>	Gulf of Maine	Dredging	Substratum change from organic-silty sand to a sandy gravel, possibly due to disruption of amphipodal tube mats	Langton & Robinson 1990
Blue Mussel <i>Mytilus edulis</i>	Limfjord, Denmark	Dredging	Sediment resuspension, and increasing the likelihood of wind damage to sub- strates	Riemann & Hoffmann 1991
Bloodworm <i>Glycera dibranchiata</i>	Bay of Fundy	Intertidal manual digging	Contributing to a decrease in sediment stability in the intertidal zone	Shepherd <i>et al.</i> 1995
Date Mussel <i>Lithophaga lithopaga</i>	Mediterra- nean Italy	Subtidal sledge hammering	Rocky substratum destructed and re- colonization of bare rock prevented by sea urchin grazing	Fanelli <i>et al.</i> 1994

Benthic organisms can substantially alter the properties of nearby sediments in a number of ways: inter-particle adhesion, grain-size distribution through the formation of (pseudo-)faecal pellets, sorting of grain-sizes, water content and

the formation of structures, all of which affect the stability of sediments with respect to fluid forces and geotechnical properties (Gray 1974, Rhoads 1974, Grant *et al.* 1982, McCall & Tevesz 1982, Probert 1984, Hall 1994). To which extent



Fig. 70. A system of healthy mussel banks south of Ameland in 1970. (photograph by Jan van de Kam)

are the large populations of suspension-feeding mussels and cockles (and indeed other invertebrates) responsible for the sedimentary characteristics of their neighbourhoods in the Wadden Sea? For example, it is well known that mussel beds locally accumulate large amounts of silt in the form of faeces and pseudofaeces (Dankers 1993, Hertweck & Liebezeit 1996), sometimes to the effect that such accumulations smother the beds themselves. Other filter-feeders such as Edible Cockles and Baltic Tellins produce similar silty products (Risk & Moffat 1977, review in Oost 1995b). But could such effects extend to whole tidal basins?

This question had the interest of J. Verwey, who, together with his coworkers, studied problems of the distributional ecology of Blue Mussels and Edible Cockles. They were concentrating on the ways by which the patchy distributions of both species in the Wadden Sea came about, e.g. by detailed studies on settlement and re-settlement patterns (Kreger 1940, Kuenen 1942, Maas Geesteranus 1942, Baggerman 1953, Kristensen 1957), but were also concerned with the effects that these common bivalves had on the general biological and sedimentary processes in the Wadden Sea (Verwey 1952, 1954). In a review, Verwey (1952:p. 227) wondered "what influence cockles and mussels are on sedimentation within the Waddensea generally"? Acknowledging the need for further detailed studies, he suggested that by filtering out large quantities of small suspended particles brought in with the currents from outside the Wadden Sea, and turning these into products that are easily deposited ([pseudo-] faecal pellets), these bivalves contribute a great deal to the sedimentation processes in the Wadden Sea. If his visions were true, and more recent studies (Risk & Moffat 1977, Aller & Yingst 1985, Smith & Frey 1985, Dankers *et al.* 1989, Jaramillo *et al.* 1992, Oost 1995b) strongly suggest and give proof that Verwey was right in believing that the bivalves *do* play a large role in sedimentation processes, then the loss of intertidal mussel banks and extensive cockle beds from much of the Dutch Wadden Sea must leave a strong imprint on current sedimentation processes. But, as usual with such quite hidden effects, it will take some time (on the assumption that the necessary studies will be carried out in the Wadden Sea) before any sedimentological changes and their consequences will be (fully) recognised.

Probert (1984) provided some heuristic models to help understand how sedimentation-related processes interact with benthic community structure [Or, rather more specifically in regard to questions about interactions between creeping crawlies such as deposit-feeding worms and crustaceans and more sedentary species such as tubeworms and bivalves, these being called suspension feeders by him. The latter category would include species like *Macoma balthica* that in current European terminology is called a 'deposit-feeder', perhaps in a more restricted sense of using the word (Kamermans 1992).] Probert starts off noting that a distinction between *natural* and *anthropogenic* disturbances is arbitrary where there is physical disturbance of the seabed, as is the case with the shellfisheries described in this report (Hall 1994, Dayton *et al.* 1995). Although his first model (Fig. 71) was developed to explain the process of 'trophic group amensalism' (i.e. that intense sediment reworking by strongly burrowing deposit-feeding organisms leads to increased sediment water content, increased roughness of the sediment-water interface, and a lowering of the shear velocity for erosion, so that newly settled larvae of suspension feeders get resuspended and buried, and so that the overlying water contains so much muck that it clogs the filtering and respiratory structures of suspension feeders; Rhoads & Young 1970), it nicely illustrates some possible interactions between sediment characteristics, benthic community organization, and disturbances in the form of dredging and/or storms. An additional model of Probert (Fig. 72) illustrates how repeated disturbances (caused by seasonally occurring storms and/or mechanical shellfish harvests, for example) could lead to an ongoing decline of sediment stability and to the disappearance of suspension feeders (*Cerastoderma*, for example). The increasingly narrow windows of opportunity for their settlement make it more and more difficult for the sediment-stabilizing species (i.e. suspension feeders) to 'correct' the temporary decreases in sediment stability (as in Fig. 71).

Thus, the 'negative biodepository spiral'-hypothesis (Fig. 17) had, albeit perhaps more biotically-oriented, equivalents in the literature. These older models invite stronger attention to the problems of sediment characteristics, hydrodynamic conditions and larval settlement and resettlement, issues that were also addressed by Verwey and associates (see references above) for

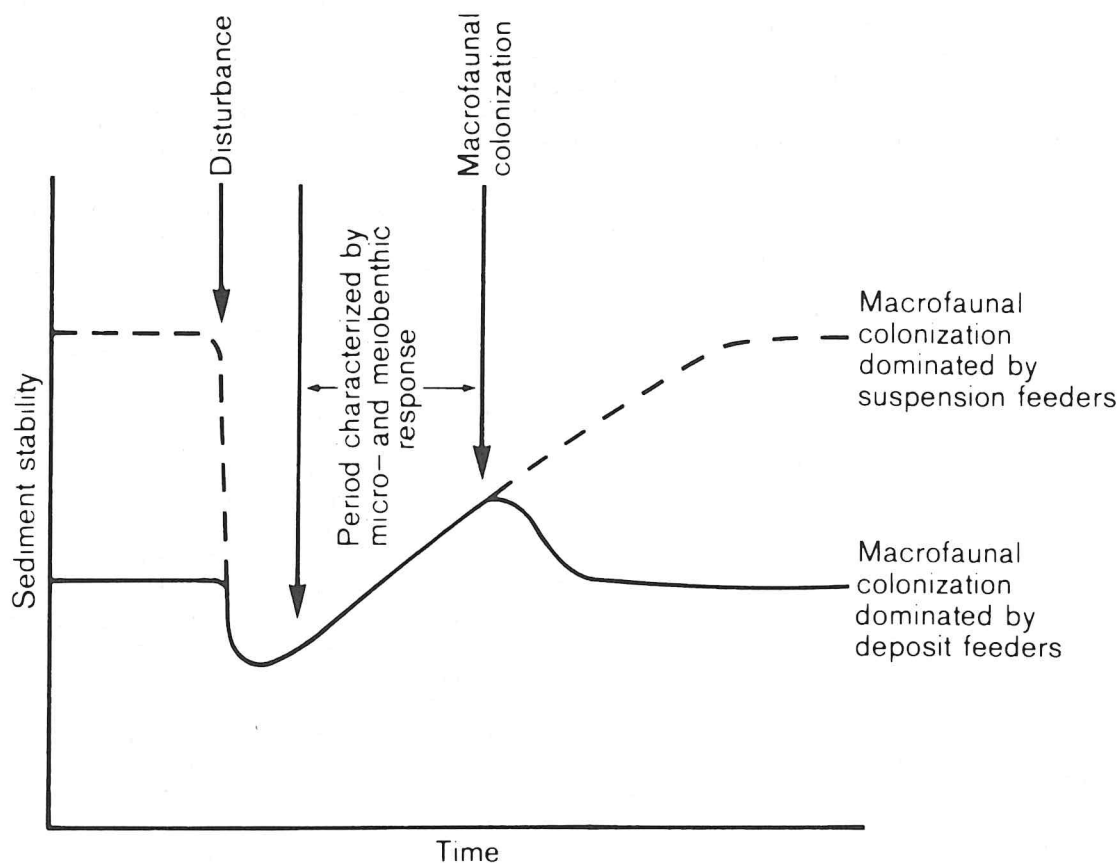


Fig. 71. Conceptual scheme of the influence of sediment stability on the timing of micro-, meio- and macrobenthic responses after a disturbance (from Probert 1984:fig.1). Here, sediment stability is used in a qualitative sense encompassing aspects of grain-size, inter-particle cohesion, sediment packing, shear strength and water content.

the Wadden Sea. Emerson & Grant (1991) documented the importance of wave action and strong currents in displacements of juvenile *Mya arenaria* (post- or resettlement), reinforcing the view that hydrodynamic conditions in no small degree determine adult distribution. Although obviously the larval and juvenile invertebrates show active habitat choice in addition to passive transport by strong currents, the importance of hydrodynamics in determining settlement patterns of soft sediment invertebrates is increasingly recognised (review by Butman 1987, Savidge & Taghon 1988). In a detailed study of the (re-)settlement patterns of juvenile *Cerastoderma edule*, *Macoma balthica*, *Mya arenaria* and *Ensis directus* in the German part of the Wadden Sea, Armonies (1996) demonstrated

that hydrography indeed plays a dominant role in the initial settlement patterns of these bivalves. Nevertheless, at least within a year after first settling the juvenile bivalves can make additional habitat-choices by their habit of byssus-drifting to other and potentially more favourable areas (Armonies 1996, Beukema 1993a, Beukema & de Vlas 1989).

On the basis of our own data and the literature we have established that there exists an intense interplay between hydrodynamic and sedimentological factors and processes of invertebrate recruitment in soft sediments. This interplay means that changes in bivalve populations, such as the ones observed in our studies on the intertidal sandflats around Griend (Chapter 4), can be (as argued before) due to local distur-

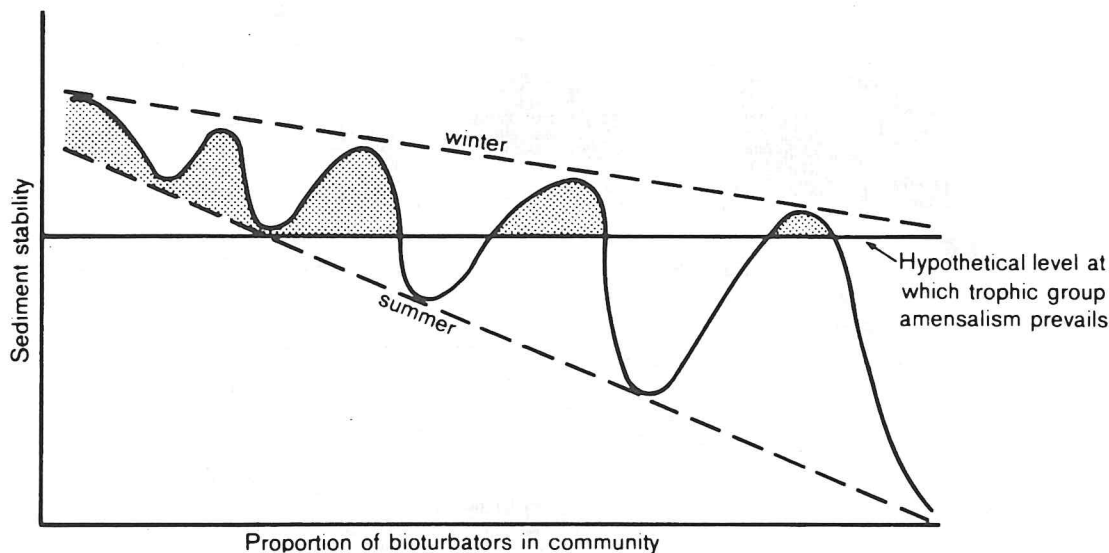


Fig. 72. Conceptual scheme, for shallow-water soft-bottom communities in temperate waters, of long-term changes in sediment stability (affected by seasonal disturbances due to storms and/or dredging) in relation to the settlement by different kinds of functional groups, juxtaposing the effects and roles of the deposit-feeding bioturbators against the rather statically living 'suspension feeders' (including sedentary bivalves and tube-living polychaetes) (from Probert 1984:fig. 2). Shaded areas represent periods available for settlement by suspension feeders. Only when the densities of deposit-feeding bioturbators is below a certain threshold (the idea of 'trophic group amensalism'), can suspension feeders invade.

bances, but also by disturbances in other parts of the tidal basin (Armonies 1996). Thus, the shellfisheries around Griend described in this report may impact the shellfish populations elsewhere in the western Wadden Sea, but equally, shellfisheries activities quite far away from Griend region can affect the benthic bivalves near Griend. On the basis of the foregoing deliberations, even in the absence of shellfisheries in other parts of the western Wadden Sea (which is not true of course, see next few paragraphs), one might still expect that areas larger than the fished portion of the Grienderwaard would be affected by the shellfisheries.

6.3. Changes of macrobenthic community structure in the western Wadden Sea?

In 1995 we extended our field studies on Knots and their benthic food resources to areas beyond the Grienderwaard (in this report we show maps of the results of 1996). West of Griend and south of Richel there are extensive

intertidal flats called the Waardgronden. Nowadays, these flats are sandy, rather poor in bivalves and quite rich in small polychaete worms such as *Scoloplos armiger* (Fig. 73), but we know that in the past this region contained rich mussel and cockle beds (Fig. 74). In the late 1930s, Kreger (1940) collected detailed information on the Edible Cockle populations in an area south of Richel immediately west of the Grienderwaard across the Vliestroom (see Fig. 1) with the fanciful name 'Staart van Schieringhals'. At the time this area was fished for cockles, collected by manual raking on a scale quite incomparable to that of today (Kreger 1939). Kreger (1940) mentions that the immense densities of Edible Cockles found in the lee of large mussel bank complexes there (Fig. 74) even showed stunted growth. Thus, in those days recruitment and survival appeared to have been no problem, even though competition for food between the different bivalve species (cf. Kamermans 1992) may have reared its tail.

For this particular area (called 'Staart van Schieringhals'), for a place further south ('Driesprong'), and for the intertidal flats south of

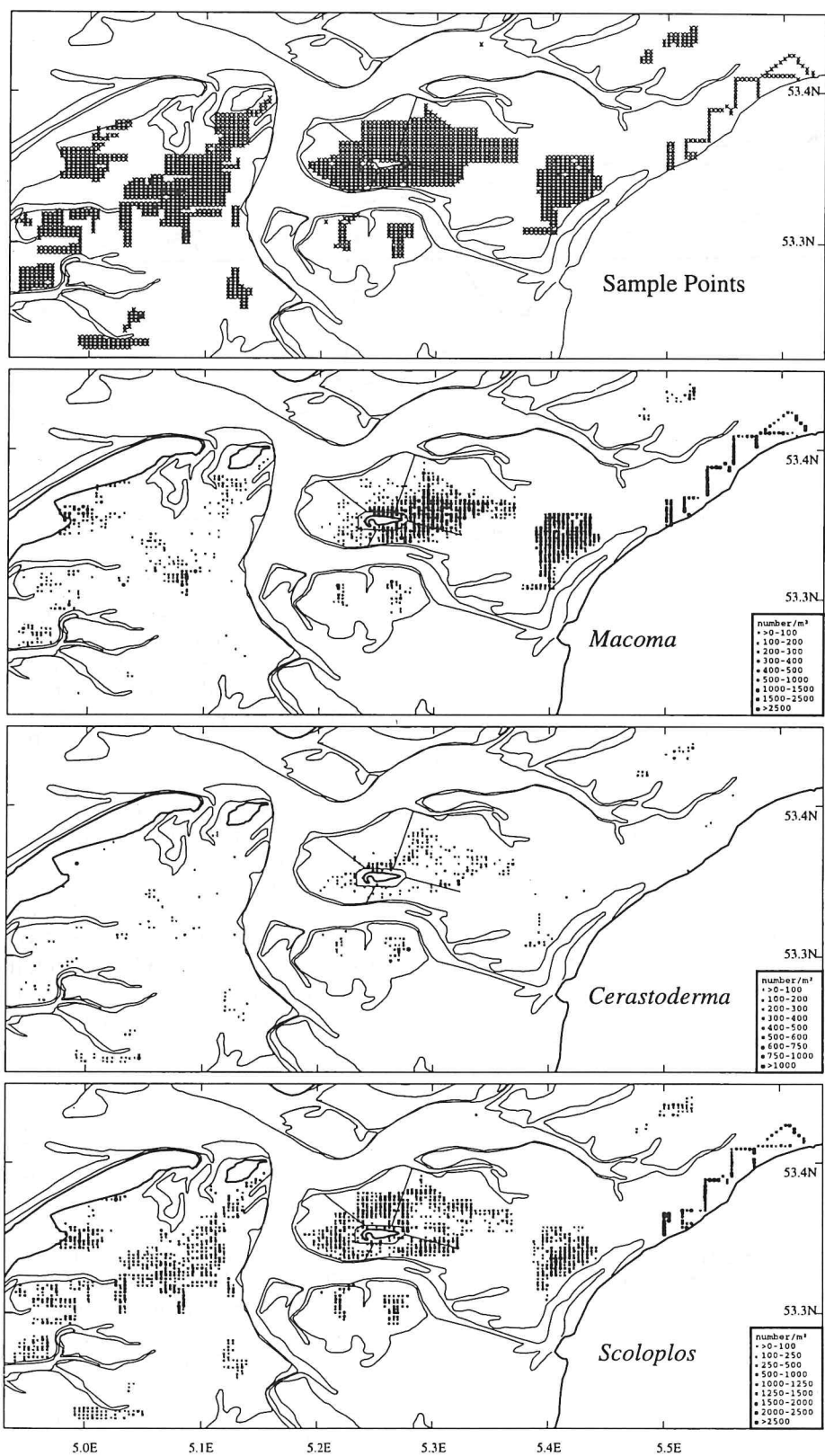


Fig. 73. Large scale patterns of numerical abundance in the western Wadden Sea in July-August 1996 of *Cerastoderma edule* (top panel), *Macoma balthica* (mid panel) and *Scoloplos armiger* (bottom panel). This is based on the more extensive surveys that the NIOZ-team of T. Piersma and co-workers tries to keep in place since 1995. The data are based on a grid-mapping approach such as carried out around Griend (Chapter 4): at each of the 2100 sites a single core of 1/56 md sieved over a mesh of 1 mm.

Griend across the Blauwe Slenk ('Langezand'), there are in fact some early quantitative data sets to compare with the one for Griend (J.J. Beukema & W. de Bruin pers. comm., see Beukema 1989), to see whether the changes in macrobenthos documented for the Grienderwaard have occurred in the surrounding areas as well. The changes since 1988 at all three areas are very similar to the changes near Griend (Fig. 75). Between 1988 and 1996 *Macoma*, *Cerastoderma* and *Nephtys* showed large decreases in numerical densities in the entire region (for *Macoma* rather unlike Balgzand, see Figs. 68 and 69). In contrast to the bivalves, the small polychaetes increased (Fig. 75), and such increases appear to be widespread over the entire international Wadden Sea (e.g. Reise 1982, Beukema 1991, 1992). In spite of their own fragility, that makes them susceptible to actual mechanical disturbances of soft-sediments including bait-

digging (Cadée 1977), small polychaetes like *Scoloplos armiger* and the Capitellids *Capitella capitata* and *Heteromastus filiformis* are particularly good colonisers of defaunated areas of intertidal sediment. Small polychaetes are characteristic of stressed and unpredictable habitats (Dauer & Simon 1976). In some polychaete species the specific reproductive strategies required for this opportunistic mode of life have been described (Barry 1989).

The abundance of small polychaetes at intertidal areas south of Richel and elsewhere, areas where formerly high bivalve stocks occurred, are in accordance with Reise's (1982) suggestion that polychaetes "are about to take over" the increasingly fishery-disturbed soft sediments of the Wadden Sea. Although some forms of shell-fisheries, such as the small-scale manual cockle harvest described by Kreger (1939), have been around for a long time now, the rapid mechani-



Fig. 74. A view from over half a century ago (ca. 1938) of the area of intertidal flats south of Richel in the western Wadden Sea (Staart van Schieringhals). Note the contours of the island Vlieland at the skyline, so familiar to the lucky ones that have participated in the fieldwork on or near Richel. This is Plate III from Kristensen (1957), based on a photo made by D. Kreger of the Koninklijk Nederlandsch Aardrijkskundig Genootschap. It shows a shallow creek inhabited by a very dense population of small-sized cockles, the stunted growth of which might have been caused by the extensive mussel banks in the background.

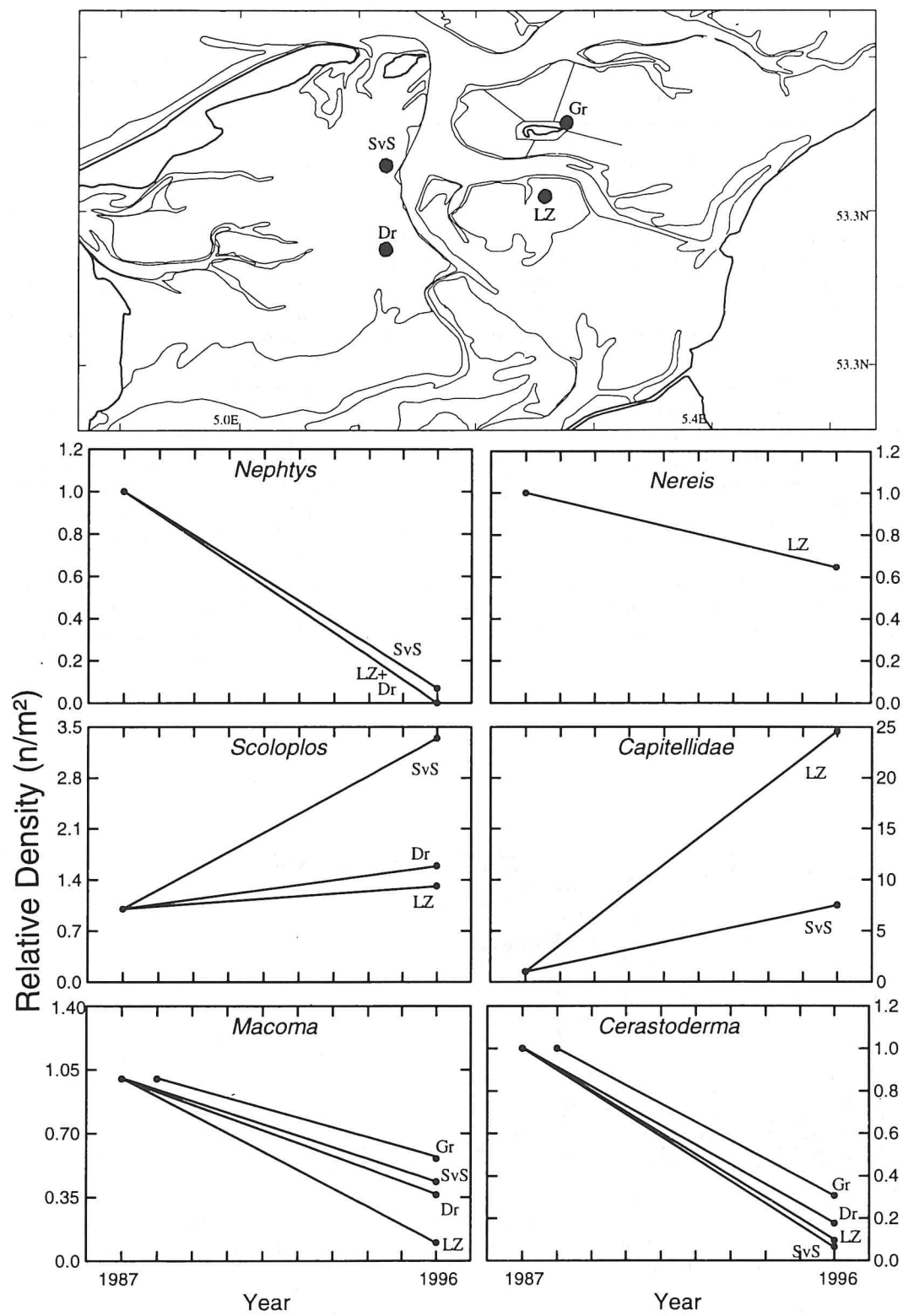


Fig. 75. Changes in numerical densities between 1987 and 1996 of six macrobenthic invertebrate species in intertidal areas around the Grienderwaard (six bottom graphs), based on surveys in the summer of 1987 by J.J. Beukema and associates (pers. comm.; see Beukema 1989) and our own surveys in July-August 1996. During the survey of 1987 four short line-transects were covered that overlapped with our 1996 grid-mapping survey (see Chapter 4). The relevant sampling locations (see map in upper panel where Gr=Griend, LZ=Lange Zand, Dr=Driesprong and SvS=Staat van Schieringhals) were chosen to overlap with the 1987 efforts as much as possible. In view of the abundance of *Macoma* brood at nearshore Griend, for this site densities were scaled to biomass values.

sation and expansion of the shellfisheries in the 1970s and 1980s must have left their mark in more ways than described for Griend for the period 1988-1996. In a correlative study, Emerson (1989) showed that wind-stressed and wind-disturbed, highly hydrodynamic shallow soft-sediment habitats had a significantly lower secondary production than calmer areas. Thus, it seems that if the shellfisheries in combination with other sediment disturbing activities such as sand- and shell-dredging, are responsible for an increasingly dynamic Wadden Sea ecosystem, nature will eventually catch up and make productive shellfish harvests impossible. But by that time not only the fishermen will have lost out, many shorebirds entirely dependent on the benthic food resources will be among the losers as well.

6.4. Effects on shorebirds?

So what about the future of shorebirds such as Knots in the western Wadden Sea? Will the sight of Knots flying along the beacon and warden's house on Griend (Fig. 76) be a sight of the future?

The first observations that we made on the intertidal flats around Griend in August and September 1988, just before the mechanical cockle-harvest, showed that Knots foraged to a large extent on the intertidal flats north of the island (Fig. 66), eating predominantly Baltic Tellins (Fig. 65). The observations on Griend made in the 1960s to the 1980s (Veen & van de Kam 1988) confirmed that the northern sectors historically provided the feeding grounds for Knots near Griend (Fig. 77). Apart from the northern sector, Knots also foraged in the east, representing the best used area from 1988



Fig. 76. A flock of Knots in flight close to the island of Griend in the 1970s: a view from the past or one of the future too? (photograph by Jan van de Kam)

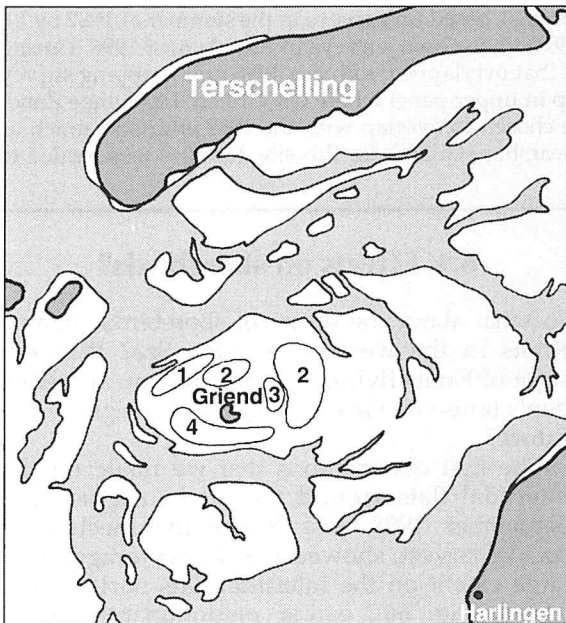
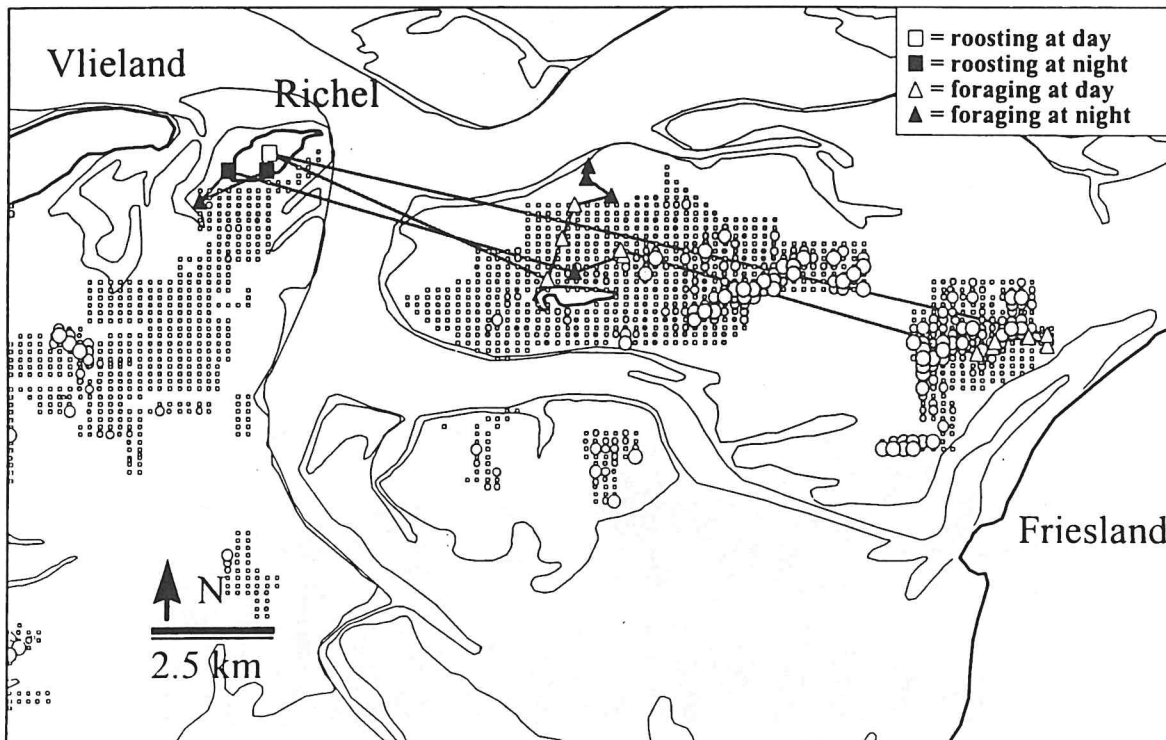


Fig. 77. Generalised feeding distribution of waders around Griend in the 1960s through the 1980s based on the observations of Jan Veen and associates. On the map of the intertidal flats around Griend, (1) indicates the distribution of feeding Oystercatchers (on the mussel banks northwest of the island), (2) indicates the feeding distributions of Knots and Dunlins, (3) the Grey Plovers and (4) the Bar-tailed Godwits (after Veen & van de Kam 1988: p.135).

onwards. Our studies on individually radio-marked Knots in the western Wadden Sea (e.g. van Gils & Piersma MS) have shown that nowa-

days Knots fly quite long distances. The birds often roosted on Richel, especially with the higher tides (Piersma *et al.* 1993a), but they only passed the Grienderwaard on their way to feeding areas close to the Frisian coast, the Ballastplaat and intertidal flats even closer to the mainland shore. Figure 78 provides an example of a typical flight pattern of Knots. In this case of a female on 22 August 1996, the bird roosted at Richel, stayed some time on the Grienderwaard to feed but spent by far the most time on the Ballastplaat profiting from high densities of suitably sized Soft-shell Clams.

That Knots, and indeed many other shorebird species including Oystercatchers *Haematopus ostralegus* and Common Gulls *Larus canus*, roost-



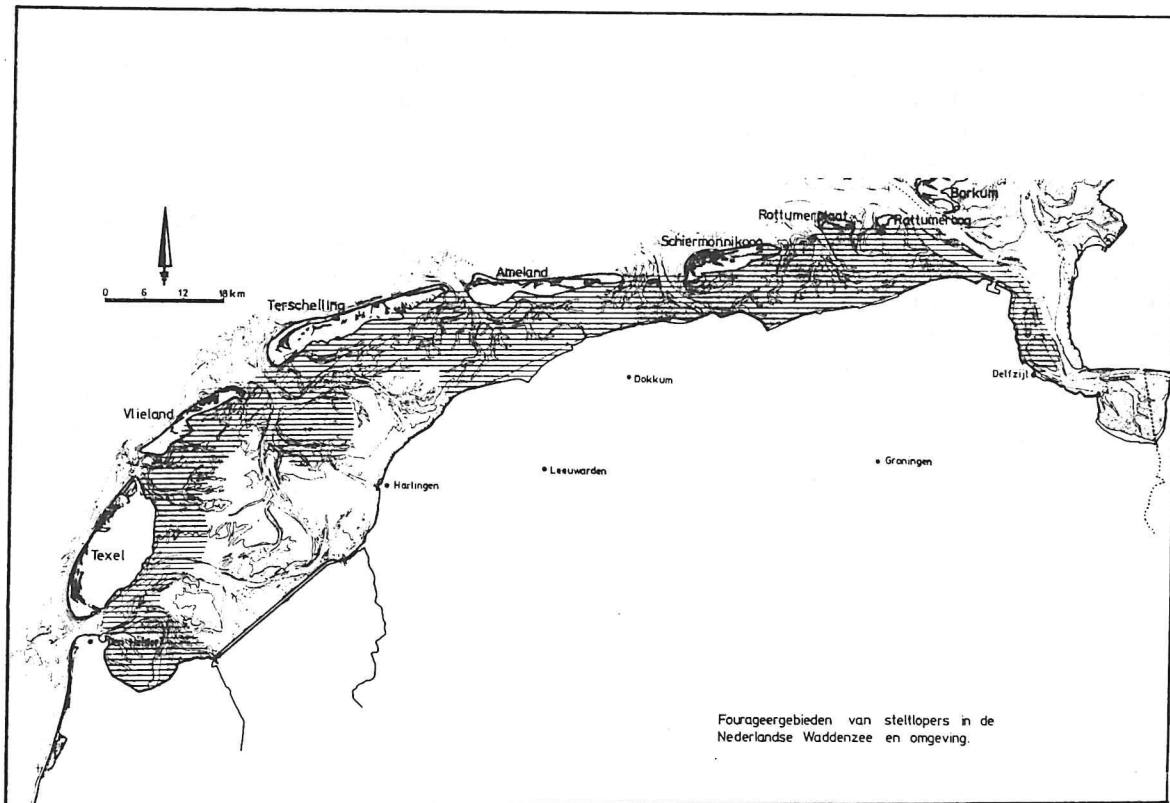


Fig. 79. Approximate feeding distribution of waders in the Wadden Sea in the 1960s showing that large areas of intertidal flat quite remote from land (areas of Driesprong and Ballastplaats, for example) were not used then (from Waddenzeecommissie 1974:p.60)

ing at Richel and Griend fly as far as Ballastplaat and the Frisian offshore flats to forage, seems to be quite a novel development. A map of the Dutch part of the Wadden Sea showing the foraging grounds of shorebirds published in 1974 (Fig. 79; Waddenzeecommissie 1974) showed that the Ballastplaat and surrounding intertidal flats, and the areas south of Staart van Schieringhals and Driesprong were the only areas not

used by shorebirds. The map probably describes the situation of the 1960s and 1970s, a time when shellfish was harvested manually but when the shellfisheries industry still had to emerge. For what we know, the underused areas of intertidal flats did have sizeable shellfish populations, which were most probably even bigger than those of today (Fig. 75), but were still not occupied by shorebirds such as Knots.

Fig. 78. Use of the intertidal flats in the western Wadden Sea as feeding grounds by an individually radiomarked Knot of the *canutus* subspecies (female #493) on 22 August 1996. The presented observations start late in the evening on the roost at Richel, after which the bird fed for a brief period immediately southwest of Richel (around 1 a.m.). During early morning high water the bird roosted on Richel (1-5 a.m.) but then flew to the Grienderwaard where she foraged for an hour. Around 7 a.m. she continued towards the Frisian coast and foraged on Ballastplaat for much of the morning before flying the more than 11 km back to Richel for another roosting period (1-5 p.m.). Later in the day she returned to Griend to feed there for the rest of the day. The movements of female #493 are plotted on a distribution map of the first year-class of Soft-shell Clams *Mya* (based on data from 2100 sampling stations, of which about 1400 are shown here, see Fig. 73). *Mya*, in the absence of harvestable densities of *Macoma*, provided an alternative prey in 1996. Five days after these registrations, #493 was recorded for the last time in the Wadden Sea during an aerial reconnaissance, probably departing for her West-African wintering grounds shortly thereafter.

Total population size of Knots wintering in Europe (the *islandica* subspecies) was then fairly similar (or slightly larger) than today (Piersma *et al.* MS3), and the wintering numbers of *canutus*-knots occurring on passage during north- and southward migration were probably quite a bit larger (see below). The only remaining explanation for shorebirds not using areas of intertidal flat far from the roost (such as Ballastplaat), is that the nearshore flats contained sufficient food so that they were able to save on the costs of transport as much as they could (cf. Zwarts 1976).

Although it is impossible to reconstruct the numbers of Knots using the Griend area in the decades before 1988, it seems certain that this

species has had to change its main feeding grounds quite dramatically over the last 30 years. Not only had the northern sector around Griend to be abandoned after 1988, over the last decade or so the birds started commuting to feeding grounds much further away from their high-tide roosts. Perhaps the extra costs of living that such flights entail (see Piersma *et al.* 1993a for some calculations) may not be directly detrimental, but it is quite possible that the higher levels of overall energy expenditure may affect Knots in more subtle ways, including the incapacity to balance their energy budgets in midwinter and the higher risks of parasitic infections due to continuous physiological stress (see below).

7. FINAL DISCUSSION: THE LARGER PICTURE

*"Typically, a few fishermen will discover a new resource one season and make significantly higher earnings than the rest of the fleet. For the next two seasons a substantial number of vessels convert to exploit the fishery. New vessels under construction in the second season enter the fleet in the third and fourth seasons. Before all of the new vessels have entered the fleet, in the fifth or sixth season, the maximum sustainable yield of the fishery has been reached or exceeded. Meanwhile, fisheries experts begin to collect statistics in the third season of the fishery. By the sixth season enough information has been gathered so that guidelines can be drafted.. Two years after overexploitation began, a low quota (but not low enough) is imposed. Many vessels leave the overexploited fishery, which is extremely slow to recover. In the meantime, ecological damage of unknown proportions has been done...." (T.F. Flannery, *The future eaters*, Reed Books, Victoria, 1995: p. 105-106)*

This description of a typical history of overexploitation (Berrill 1997), was written with an Australian setting in mind and for an Australian audience. But how familiar is the theme! And although time scales may differ, doesn't the tragic quote also encapsulate the story of shell-fisheries in the Dutch Wadden Sea?

7.1. Coastal seas: protected by law, but outlawed by fisheries management?

In the 1950s-1970s, a surge of plans to reclaim large parts of the Wadden Sea for agricultural, military and recreational purposes (e.g. van der Burgt 1965) coincided with a surge in public interest in (Abrahamse *et al.* 1976), and studies of (Wolff 1983) the nature of the Wadden Sea, including migratory waders and other water-birds. A national enquiry into the pros and cons of these large infrastructural plans incorporated a brief evaluation of the known biological values (Waddenzeecommissie 1974). At that time, the ornithological information on the Wadden Sea was largely based on the efforts of amateur workers organised in the federations of young naturalists (for example the 'Schierboeken', e.g. Vogelwerkgroep NJN 1970, 1974) and the exploratory academia-based studies of Boere and coworkers (e.g. Boere 1976). Large reclamation plans being rejected, and the threat of large-scale water pollution slowly being curtailed by bans at the sources (e.g. Wolff 1992, Bakker *et al.*

1994), activities to protect the natural values of the Wadden Sea by formal legislative measures rapidly gained momentum (van der Zwiëp 1992, de Jong 1994, Jepsen 1994). By 1988, the Dutch Wadden Sea had been awarded the international *Ramsar* status (see Smart 1987), many parts were protected under Dutch national nature conservation laws, specific parts had been assigned special reserves such as 'Stiltegebieden' (quiet areas, areas of stillness). At the Dutch national level, management agreements to conserve and enhance the natural values of the Wadden Sea area were reached in the Planologische Kernbeslissing (PKB) of 1992. Also, a national panel of involved parties, the Waddenadviesraad, was established. Internationally, nature conservation and other management issues received coordination through the Trilateral Wadden Sea co-operation (de Jong 1994).

Yet, all these protection measures did not lead to a full protection of the biological richness and biodiversity of the Wadden Sea. Tourism kept on expanding, agricultural activities on the islands and along the mainland coast and fishery activities on the sea kept on intensifying, whereas military training practices continued, and the hunt for fossil fuels was re-opened. Of course, given the long history, a certain amount of human activity should be permissible, and under the *Ramsar* Convention human 'wise use' is actually permitted if not encouraged. However, it seems debatable whether industrial fish-

eries, exploration and exploitation of fossil fuels and military training practices fall comfortably within any definition of 'wise use'. In any case, the studies presented in this report give no reason to think that modern fishery methods can claim to be sustainable. Bottom-fisheries may be an economically profitable trade, it may not be a wise way to use the Wadden Sea in ecological terms.

7.2. Encroaching humans: gradual loss of habitats and endemic species

Human fishery activities are no doubt as old as the present Wadden Sea (Abrahamse *et al.* 1976), but the scale and the intensity of the fisheries has shown dramatic increases over the last 100 years, and especially over the last 30 years. Mussel-'farming' has been around since the specialists from the province of Zeeland moved in during the early 1960s. This industry not only involves the filling up and dredging out of the artificial subtidal mussel beds, it also entails the bringing together of mussel spat from much larger areas, including the intertidal zone. Cockles have not been a popular food in The Netherlands, but the demands by foreign markets (initially mainly England) nevertheless made this fishery profitable (albeit on a limited scale) from the early 1900s onwards (e.g. Kreger 1939). With the discovery of new markets (notably the countries in the Mediterranean region) and the development of mechanical harvesting techniques this fishery has, over the past decades, seen a large expansion. The data presented in this report strongly suggest that the Wadden Sea ecosystem has not been able to cope with the combined effects of modern mussel-farming and cockle-dredging techniques. The state-of-the-art shellfisheries of the Wadden Sea are thus far from sustainable and the ecological values upon which they are based appear to be under immediate threat. The intertidal flats (and probably the understudied subtidal flats as well) together with their living communities appear to slowly erode into oblivion quite literally.

The quote introducing this chapter illustrates that 'unsustainability' leading to ecological crises in the harvested seas is a *very* common phenomenon (Berrill 1997, Roberts 1997). Overexploitations leading to ecological collapses are common practice worldwide and are

close to the norm in the Wadden Sea as well. Earlier this century the intense oyster-fisheries have led to the extinction of Edible Oysters *Ostrea edulis* in the Wadden Sea (Reise 1981). This process has repeated itself at the other side of the Atlantic, in Chesapeake Bay, the largest estuary of the United States of America and a region that shows many similarities to the Wadden Sea. Just as in the Wadden Sea, a virus pandemic in the 1930s exterminated most of the submerged seagrass, taking with them a rich and biodiverse marine community. Just as in the Wadden Sea, the greater turbidity of the waters (perhaps in combination with herbicide run-off from the surrounding farmland) has prevented the seagrass beds from returning in any numbers. In the course of the last 100 years an important shellfish resource, the Eastern Oyster *Crassostrea virginica*, became overharvested (Rothschild *et al.* 1994, Lovejoy 1996). As the oyster fisheries developed, the physical integrity of the oyster banks was damaged by oyster-fishing gear. Subsequently, the oysters lost much preferred habitat as a result of sedimentation. After a long-term decline since the early century, eventually, in the late 1980s, the harvests crashed completely. Although short harvesting seasons and a few sanctuaries have now been implemented, with 1% of the previous stocks remaining, little has been left to protect in Chesapeake Bay.

Several species other than Edible Oysters have disappeared from the Wadden Sea, and in many cases human exploitative activities appear to be involved. For example, the disappearance of the extensive reefs formed along tidal channels by the tube-living polychaete *Sabellaria* are likely to have been scraped away by the trawling actions on shrimp and perhaps other fisheries (Reise 1982). The decline and eventual extinction of the Whelk *Buccinum undatum* (a large gastropod), in the Wadden Sea was kicked off by intense fisheries in the first half of this century, even before any pollution problems showed up (Cadée *et al.* 1995). A small snail like *Rissoa membranacea* went extinct when its habitat, subtidal seagrass meadows, disappeared from the Wadden Sea (Cadée 1997). Although the fisheries were probably not responsible for the disappearance of the seagrass beds, they might well help to prevent their re-establishment (de Jonge *et al.* 1997). One really wonders whether the recent reductions in the stocks of

intertidal Blue Mussels and Edible Cockles, the former of which may, at earlier times, have benefited from the disappearance of food-competing oysters (Reise 1982), may signal the first beginning of another series of extinctions. Perhaps it is hard to believe that cockles and mussels might disappear from the Wadden Sea, but so was the disappearance around the turn of the century of Edible Oysters that so much affected the fishermen of Texel (van der Vlis 1975). It is striking that an anonymous fisheries-report of 1911 (van der Vlis 1975:p. 200) claimed that the crash of the oysters in the Wadden Sea was due to sedimentological changes.

What seems to be going on is a rather continuous decrease in the abundance of bivalves and a concurrent increase in the abundance of several polychaete species, processes that may extend as far back as 1880. Summarising the extensive and detailed faunistic information from the Sylt area in the northern part of the Schleswig-Holstein Wadden Sea dating back to the late last century, Reise (1981) came to the conclusion that whereas bivalves and some other groups show long-term decreases in species diversity, especially the smaller polychaete species with short life spans are doing well (Table 2). As we have discussed above, such polychaetes take rapid advantage of environmental disturbances leading to faunal depletions such as oxygen depletion in hot summer periods, severe cold in harsh winter periods and heavy local pollution. Reise (1982) attributes the disappearance of 28 common macroinvertebrate species to the loss of the many microhabitats provided by the complex physical structures

TABLE 2

Long-term changes for the period 1869 to 1981 of 100 macrobenthic species common at one time or another in the Wadden Sea area close to Sylt, Schleswig-Holstein. This table gives the numbers of species showing either a long-term decrease, no change or an increase, and is modified from Reise (1982).

Taxonomic grouping	Decrease	No change	Increase
Bivalves (Bivalvia)	8	3	1
Other molluscs (Gastropoda & Placophora)	1	7	3
Crustaceans (Crustacea)	6	12	8
Other invertebrates (Porifera, Coelenterata & Echinodermata)	8	7	0
Polychaete worms (Polychaeta)	5	13	18

such as oyster beds, *Sabellaria* reefs, and seagrass (*Zostera marina*) beds, and notices that of the 30 species showing a long-term increase, half are particularly abundant in mussel banks, a habitat that has only disappeared over the last decade. When these complex intertidal structures that provide shelter, nutrition and several other favours (Table 3) disappear, so does the fauna that associate with them.

TABLE 3

List of environmental factors responsible for the high species diversity in physically complex habitats such as oyster and mussel banks, *Zostera* beds and *Sabellaria* reefs, relative to the low species diversity of the bare sand flats that are left after their destruction. Based on Boström & Bonsdorff (1997).

Factor	Complex habitat type	Bare sand flat
Habitat complexity	High	Low
Shelter	High	Low
Flow velocity	Low	High
Deposition	Enhanced	Reduced
Sediment	Fine	Coarse
Sediment stability	High	Low
Organic content	High	Low
Food availability	High	Low

7.3. One problem of sustainability: declines of reproductive capacity of bivalves?

Below certain threshold densities the reproductive capacity of free-spawners (animals that simply release their gametes [eggs or sperm] in the open water, such as the bivalves of the Wadden Sea), may suddenly collapse. This could be due to several non-mutually exclusive causes: (1) fertilisation problems of low adult densities of free-spawners (Levitan & Petersen 1995, see Jennings 1997), and (2) reduced survival during the first year as the starving avian predators cue in on the scarce resources (Beukema 1993b, pers. obs.).

Free-spawners run the risk that their gametes are diluted to the extent that they don't meet up with their complements. Proximity requirements for adults may be such that they must be within less than a meter of each other at spawning (Denny & Shibata 1989). Thus, free spawners living at low population densities or spawning out of synchrony, may incur very low fertilisation rates of the eggs. In an overex-

exploited gastropod species from the Californian coast, low densities and the possible occurrence of 'sperm limitation' may have led to their near extinction (Tegner *et al.* 1996). The recent decreases in *Macoma* populations, even in parts of Balgzand, could in theory be indicative of a downward spiral in which continually declining densities lead to continually decreasing fertilisation rates, leading to further population declines. Similar processes are possible for species like Edible Cockles, and even Blue Mussels. Indeed, one of the big and very difficult scientific issues that needs cracking in the near-future is the complex of factors responsible for the survival of the free-swimming larval stages. It is clear that during this pelagic phase important processes take place, but it is equally clear that we have very little insight as to what processes determine the size of the settling stock (e.g. Roughgarden *et al.* 1985, 1988, Hedgecock 1994, Neill *et al.* 1994). We just don't know.

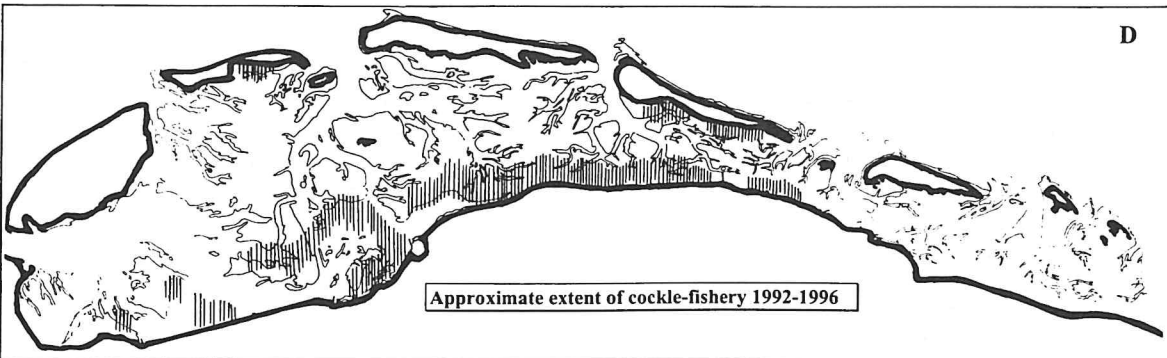
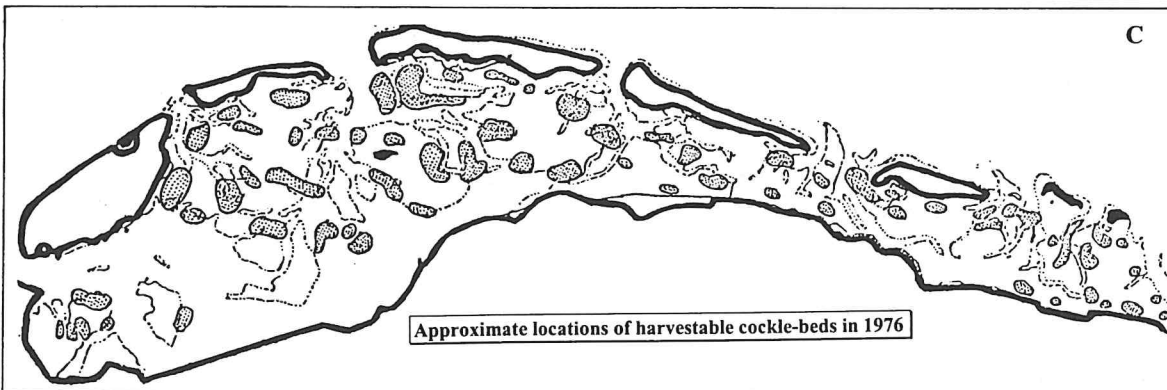
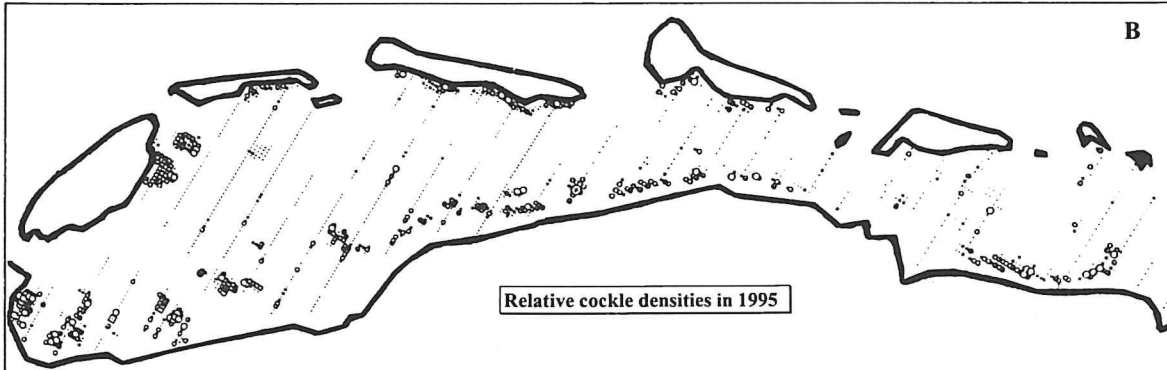
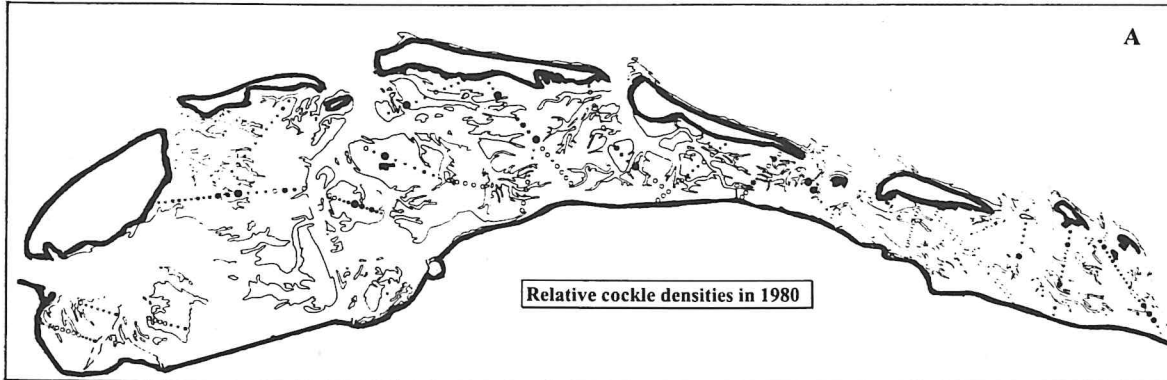
During a decline of the population, the reduced numbers of juvenile bivalves trying to settle on the intertidal flats, and subsequently trying to outgrow (*Cerastoderma*) or outbury (*Macoma*) their avian predators, may be faced with hordes of hungry shorebirds coalescing at the last remaining patches of shellfish. The complete predation by Oystercatchers, gulls and other shorebirds of the remaining small patches of Edible Cockles at an early stage of their life, seemed to take place at several spots in the western Wadden Sea in August-October 1997 (pers. obs.). In a slightly different form, the same sort of process occurred when Oystercatchers at Balgzand depleted the stocks of *Macoma*, *Mya* and *Cerastoderma* to a much greater extent than usual when, in 1990, their main shellfish resource (*Mytilus*) had been taken away by fishermen (Beukema 1993). Thus, shellfish species fed upon by relatively resilient and long-lived shorebirds might quite easily be kept rare. Why don't we know more?

7.4. Effects on genetic population structuring of bivalve populations?

Between 1980 and the mid 1990s an intriguing change in the distribution of Edible Cockles over the intertidal flats of the western Wadden Sea took place (Fig. 80). In 1976 and 1980 we find a situation that seems characteristic for what is known from earlier times (Dankers & Beukema 1983): the highest densities of Edible Cockles are found in the central parts of the western Wadden Sea, at the extensive sandy flats in the central parts of the Wadden Sea. In the 1990s the picture has changed dramatically (Fig. 80): the cockles are now found quite close to the shores of the islands and the mainland, and have disappeared from the central regions. In contrast to the past, in the 1990s the mechanical cocklers do their fishing also along the edges of the western Wadden Sea (Fig. 80D). By moving shorewards (and in spite of the possibility that the muddiness of these areas has also decreased somewhat), Edible Cockles seem to have changed their habitat preference, from the rather sandy to the rather silty. If substrate selection during settlement is a deeply ingrained life history trait (e.g. Butman 1987), then a different 'kind of' cockle is now living in the Wadden Sea than before. We propose that the 'sand-cockle' has gone extinct and the 'mud-cockle' has had a chance to get established. This hypothesis involves that, during the presettlement -free-living larval- phase of the cockles, the two morphs would be in competition (as it is otherwise impossible to explain the previous rarity of cockles in the nearshore muddy habitats). With the disappearance of the 'sand-cockle' (through overexploitation, possibly in concert with habitat changes) larval 'mud-cockles' would have gotten all the resources to themselves and could take over.

Even formulating this hypothesis may sound to some biologists (pers. comm.) like swearing in the church, but remember that there is an increasing number of studies that have docu-

Fig. 80. Changes in the distribution of Edible Cockles *Cerastoderma edule* in the Wadden Sea between the 1980s and the 1990s. (A) shows that in 1980 the relative biomass densities are consistently highest in the central parts of the tidal flat systems (based on de Vlas 1980:p.69); (B) shows that in 1995 the relatively highest biomass densities have shifted to close to the mainland and island shores (from Kesteloo-Hendrikse & van Stralen 1995:pp.22-23; note that latitude is scaled larger in the eastern half of the Wadden Sea, from Ameland eastwards); in (C) the stippling shows the approximate extents of harvestable cockle beds in 1976, mainly on the centrally lying flats (based on a survey by the 'Directie van de Visserij', reported in Boschieter 1981:p.57); in (D) the vertical hatching shows the approximate extent of cockle fishery activities in 1992-1996, especially close to the mainland shores and Vlieland and Ameland (J. Holstein pers. comm. to M. van Dijke, NIOZ).



mented fishery-induced changes in life-history characteristics and genetic profiles of target species (e.g. Rijnsdorp 1992, Avise & Hamrick 1996). The selective harvest of particular categories of a species can provide a strong selection pressure. At least in one case (of a fish, Smith *et al.* 1991), this has led to the loss of genetic diversity. It might also lead to genetically based changes in life-history strategies, such as habitat choice during larval settlement. Again, we just don't know.

Whatever has happened, the changes in the distribution of Edible Cockles has made them very susceptible to the effects of severe winter periods. Whereas in the central parts of the Wadden Sea the dynamics of the water and the absence of structures for attachment ensure that ice floes move around during long periods of subzero temperatures, such as during the recent winters of 1995/96 and 1996/97, near the coast the ice cover only grows and remains firmly fixed for long periods of time. This ice cover easily kills off species like *Cerastoderma*, and this is what happened over the past few winters. If fishery-pressures indeed pushed cockles to the coast, the shellfishery industry has made their own target species much less resistant to these environmental perturbations. They have also made cockles, still an important food source for shorebirds, very susceptible to ice cover during winter.

7.5. Subtle, and not so subtle, consequences for migrating shorebirds: domino effects

Severity of winter weather, and lack of food, both resulted in enhanced mortality of the Oystercatchers of the Wadden Sea (Camphuysen *et al.* 1996, Zwarts *et al.* 1996). With the current nearshore distribution of Edible Cockles, an important food for Oystercatchers, it seems that the effects of winter weather on Oystercatcher deaths can only increase. Mass deaths of Oystercatchers along the Dutch beaches (Camphuysen *et al.* 1996) and in the Dutch Delta, and the recent halving of the breeding populations of Oystercatchers in many areas (J.B. Hulscher pers. comm.) provide the more visible signals of an intertidal ecosystem under threat.

Many species spend only part of their annual life cycle in the Wadden Sea, and Knots provide

a typical example of this lifestyle. It seems unlikely that any effects of fishery-induced food shortages would be directly visible. The birds would either go to other areas, or try to make the best of a difficult job, for example by flying longer distances between roosting sites and feeding areas (Chapter 6.4). If such compensatory mechanisms would not be good enough, such that changes in habitat and food abundance would result in only small decreases in the rates of fueling relative to those that can be achieved under normal conditions, whole cascades of effects on the population level can be the result, the 'domino effects' (Fig. 81, and see Piersma 1987). The reason for quite serious negative effects on population levels of rather small changes in achieved fueling rates, stems from the nonlinearity of many of the critical processes (Fig. 81, lower panels). The reason that such effects would never be observed at the very places where the ecological problems occur, is that in such long-distance migrants, the bones will be picked only during and after the onward flights.

The significance of the model in Fig. 81 is that it explains how relatively small habitat-induced effects on fueling rates somewhere along the migratory route may have large repercussions elsewhere, so let's examine it in more detail. Panel (A) shows the changes in body mass (or relative energy stores) over time for a population of birds that migrates from a 'departure area' to a stopover site for a second fueling period, to continue to an area of destination (see Piersma 1987). The model could refer to a northward migration (destination = breeding area) as well as to a southward migration (destination = wintering area). There is a 'natural' amount of variation among individuals in the rates of mass gains. Panel (B) illustrates the effects of problems during the first and/or second fueling episodes. The average rate of mass gain decreases, the top speeds no longer occur, and the statistical distributions of mass gain values get broader (see C, D and E for the frequency distributions of body mass values at departure or after arrival for situations without and with habitat deterioration) and lowest rates of mass gains in the population get markedly lower. During the first and second migratory flight, the accumulated energy stores don't suffice any longer and a proportion of birds dies from exhaustion/emaciation before the second fueling area or

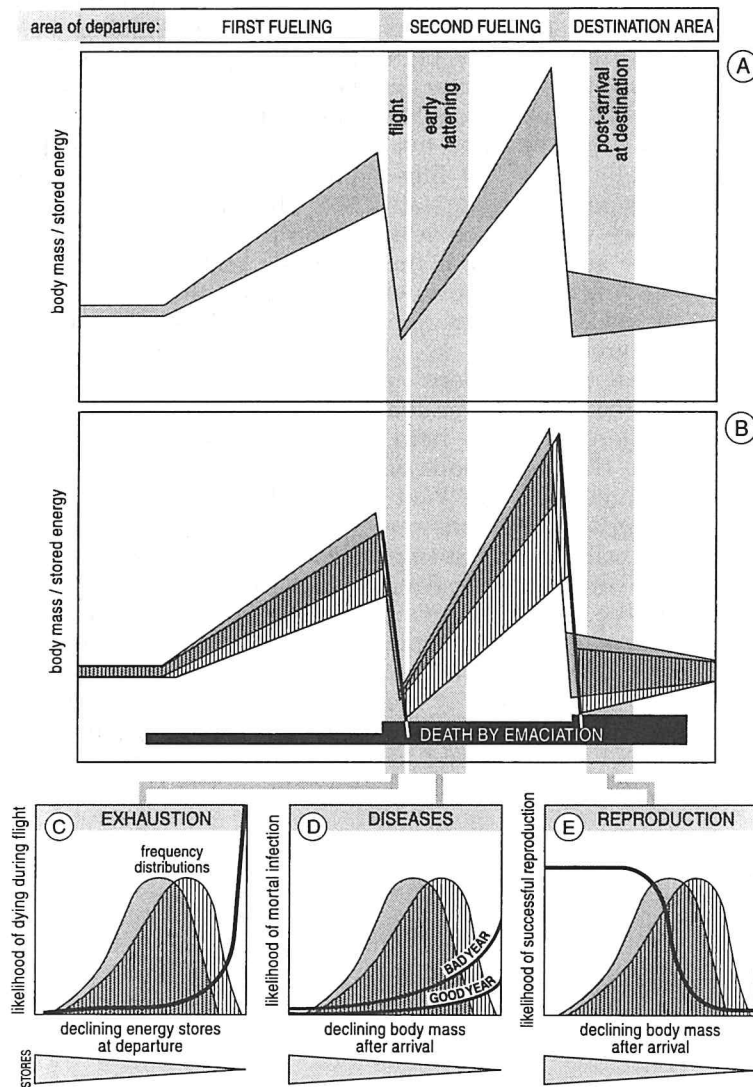


Fig. 81. Graphical model of the long-term and long-distance 'domino' effects (on migrating shorebirds) of habitat deterioration affecting the rate of fueling (decreased food abundance (longer working days (reduced ratio income/expenditure) at a departure area or a stopover site. See text for explanations of the different panels.

destination is reached. Panel (C) illustrates how the non-linear increase in the likelihood of dying during a migratory flight with decreasing body mass at departure might disproportionately affect mortality due to migration. Panel (D) illustrates that birds arriving with low body masses and trying to win back the mass and time delays might run disproportionately high risk to get infected by dangerous parasites or pathogens (Piersma *et al.* MS2), with possible differences between years depending on environmental conditions. Finally, panel (E) illustrates that if birds arrive in a poor energetic state on the destination area, they would have very small chances to reproduce successfully if the destination area is the breeding area (or survive a moulting/wintering period if the destination area refers to the wintering grounds).

Is there any evidence that the reductions in the bivalve populations in the western Wadden Sea that have hit the Oystercatchers so hard, have had similar effects on the populations of long-distance migrating shorebirds in the Wadden Sea? It comes as no surprise that the answer is, yet again, that we don't really know. It is suggestive, however, that the counts on the Banc d'Arguin in Mauritania (the most important West African wintering area, Smit & Piersma 1989) in early 1997, show that since the last counts in 1979/1980 numbers of Knots of the *canutus* subspecies have reduced by 42% to only 230,000 individuals, and that numbers of Bar-tailed Godwits *Limosa lapponica* have declined

by 47% to 343,000 birds (T.M. van Spanje *et al.* pers. comm.). Both species feed on small shellfish and migrate through the Wadden Sea to and from the Siberian breeding grounds. In contrast, Siberian-breeding Curlew Sandpipers *Calidris ferruginea* showed an increase of 36% to 226,000 birds, and the Dunlins *Calidris alpina* on the Banc d'Arguin (that breed in Iceland and Greenland) showed an increase of 18% to 921,000 birds. The latter two species both rely on small polychaetes for their food, and it is the small polychaetes that do rather well in the Wadden Sea. Thus, the repercussions of habitat deterioration in the Wadden Sea could well be severe (Fig. 81), and the few data points that allow us to examine the case indicate that the consequences of the shellfish reductions might in fact be as severe as for the rather resident Oystercatchers.

In conclusion, we note that the present ecological problems identified for the Wadden Sea are not necessarily limited to the Wadden Sea. Many British estuaries, including very important ones such as the Wash, Morecambe Bay and Ribble, are under threat from mechanical shellfisheries as well (e.g. Clark 1996, and Godwit - Newsletter of the Liverpool Bay Wader Study Group 5, Sept. 1997). The internationalisation of the world's fisheries (Berrill 1997) could bring any intertidal and subtidal area of soft sediment under threat, with all the outlined repercussions for marine biodiversity and international migratory shorebird populations.

8. EPILOGUE

"The task of preserving ecosystem integrity is challenging. Even when not influenced by human activities, ecosystems show a high degree of variability, at different temporal and spatial scales..... This inherent variability often makes it extremely difficult to separate the relative effects of natural and anthropogenic perturbations. However, absence of (scientific) evidence should not be interpreted that environmental impacts are absent. There are costs in assuming an effect of human activity on ecosystem integrity when there actually is none, but the consequence of assuming no effect when there really is one is often far greater Waiting for a scientific consensus may delay any decision about conserving the environment, with possibly irreversible consequences." (G.A. De Leo & S. Levin, *The multifaceted aspects of ecosystem integrity*, Conservation Ecology 1 (1), 1997, an 'online' scientific journal of the Ecological Society of America, available at <http://www.consecol.org>)

Based on his own research experience in the Wadden Sea of Schleswig-Holstein and assimilating results of studies made in the area by his predecessors, Reise has demonstrated the continuing loss of the original biodiversity in this region (Reise 1982, 1985, 1990, Reise *et al.* 1989; and see Table 2). He argues that, in view of the multiple causality of factors affecting tidal ecosystems including modern coastal architecture, fisheries, species introductions and eutrophication, managing any particular resource in isolation is logically impossible. He therefore recommends that entire tidal basins are set aside as self-sustaining ecological units to let them develop along their natural path in the absence of any direct exploitation ('zero-use reserves'; Reise 1992, 1994). This quite radical view contrasts with more optimistic visions expressed by several Dutch scientists (de Vlas 1992, Essink 1992, Dankers 1993, Dankers & de Vlas 1994). Even though acknowledging the common goal *"to achieve, as far as possible, a natural and sustainable ecosystem in which natural processes proceed in an undisturbed way"* (adopted by the Ministers of the Wadden Sea countries in 1992), these authors do not go so far as to exclude all so-called 'sustainable' human activities, including mechanical shellfisheries. Whether or not the more optimistic outlook of Dutch scientists has prevented the Dutch government from preventing the excessive shellfisheries' damage done to intertidal flats in 1988-1990, remains an open question.

Our studies have made very unlikely, however, the assumption that mechanical shellfisheries at the scale of the 1980s allow *natural processes to proceed in an undisturbed way*. The long-term loss of inter- and subtidal benthic biodiversity, often in direct connection with particular fishery developments (e.g. Reise 1982, 1986, Dayton *et al.* 1995, this report), and the demonstrated or probable (indirect) effects on worldwide shorebird migrants depending on these resources (this report), call for extreme caution from now on. This caution should replace the missed chance of *precaution*, formulated as part of the Rio Declaration on Environment and Development in 1992, and so enthusiastically endorsed by the Dutch government: *"Where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as reason for postponing cost-effective measures to prevent environmental degradation"*.

Postcaution should be expressed in immediate measures to protect the Wadden Sea from further damage and in actions leading to a further understanding of this ecosystem's apparent fragility and recovery potential. For example, the time seems ripe to seriously revamp Verwey's 'old' (1952) research questions on the interrelationships between suspension-feeding bivalves and the sediments they live on and in and that they produce.

9. CONCLUSIONS/CONCLUSIES

1. On 26 and 27 September 1988, during a stormy period with spring tides, suction-dredging cockle-ships reworked large areas of intertidal soft-sediments north of Griend, also the high flats close to the island. The usual deep layer of large shell fragments had been ploughed to the surface where also many dead and dying Baltic Tellins *Macoma balthica* were found. Due to the large shell fraction of the surface sediments, core sampling was almost impossible even at locations where such sampling had been perfectly successful a few weeks before.
2. The beds of Blue Mussels *Mytilus edulis* that embraced the western intertidal flats of Griend since a long time were fished away over the autumn and winter seasons of 1989-1990. Nothing of these old mussel banks remained in 1991.
3. Median grain-size values of the surface sediments increased, and silt contents decreased, between 1988, 1992 and 1994, and leveled off, or very slowly returned to earlier values, thereafter.
4. The shellfisheries-factor is the only one that can satisfactorily explain both the changes in sediment characteristics over time and the differences in these changes between the various geographical sectors around the island.
5. We thus conclude that the removal of large stocks of filter-feeding bivalves in combination with the reworking of originally rather stabile sediments, and the removal of a protective ring of mussel banks in combination with increases in tidal prism and currents, induced a cascade of effects leading to sandier sediments around Griend, and also elsewhere in the Wadden Sea.
1. Op 26 en 27 september 1988, tijdens een stormachtige periode, werden grote delen van het wad ten noorden van Griend over de kop gehaald door mechanische kokkelvisserij, die er door de springvloed in slaagden de hoge platen vlakbij het eiland te bereiken. De schelpplaat was op veel plaatsen naar boven geploegd en overal lagen dode en stervende nonnetjes *Macoma balthica*. Omdat er zich zoveel schelpresten in de top laag van het wad bevonden was het haast onmogelijk om de bodemfauna te bemonsteren met een steekbuis en een zeef; en dit op plaatsen waar we een paar weken eerder dit werk zonder moeite hadden volbracht!
2. De grote oude mosselbanken (*Mytilus edulis*) die al tientallen jaren de westelijke wadplaten bij Griend 'omarmden' werden in 1989-1990 opzettelijk volledig weggevist.
3. De mediane korrelgrootte (en het slib-gehalte) van de wadsedimenten rond Griend namen statistisch significant toe (respectievelijk af) tussen 1988 en 1992 (en 1994). Afhankelijk van hun positie ten opzichte van het eiland bleven ze daarna gelijk of keerden ze langzaam terug naar de waarden van 1988 van voor de schelpdiervisserij.
4. De genoemde schelpdier-visserij activiteiten zijn de enige factoren die op een consistente manier de veranderingen in sediment-karakteristieken in de tijd en de verschillen in die veranderingen tussen de plekken rond Griend kunnen verklaren.
5. Wij concluderen daarom dat het wegvissen van grote aantallen filterende tweekleppige schelpdieren in combinatie met het omwoelen van oorspronkelijk tamelijk stabiele wadsedimenten, en het weghalen van grote mosselbanken in combinatie met toenemende waterdieptes en stroomsnelheden, een hele serie van effecten veroorzaakt die tot zandige sedimenten leidt, niet alleen bij Griend maar ook elders in de Waddenzee.

6. The populations of benthic bivalves (notably Edible Cockle *Cerastoderma edule* and Baltic Tellin) showed large decreases in the western and northern sectors, both of which were affected by shellfisheries, but showed smaller decreases in the eastern sector (little or no fishing) and small increases in abundance in the southern sector (provision of lee by an expanded island, and increasingly silty sediments).

7. Knots *Calidris canutus* kept away from the western and northern sectors after 1988 and increased their use of the southern sector, in good correspondence with changes in food (small shellfish) abundance. However, over the last seven years their use of the Grienderwaard was only a fraction of what it has been before the shellfishery incidents.

8. In contrast to Griend, stocks of Edible Cockles and Baltic Tellins at Balgzand (a less-exposed area of intertidal flats where fewer sedimentary disturbances occurred than near Griend) rebounded after fishery-induced minimum values in 1991.

9. Our data, and an extensive peer-reviewed literature, show the intimate links between hydrodynamic and sedimentological factors, and recruitment and standing stocks of invertebrates at soft-sediments. Amongst other things, this interplay means that changes in bivalve populations, such as the ones observed in our studies on the intertidal sandflats around Griend, can be due to local disturbances but also to (human) disturbances in other parts of the tidal basin.

10. The benthic assemblages of the intertidal flats near Griend, and elsewhere in the Wadden Sea as well, seem to shift from biomass-rich bivalve-dominated communities to biomass-poor communities where short-lived but powerfully colonising species such as small polychaete worms dominate.

6. De bestanden van de talrijkste schelpdieren, kokkels *Cerastoderma edule* en nonnetjes, namen sterk af in de westelijke en noordelijke wadplaten rond Griend (die beide onder invloed van de visserij stonden). Ze namen minder af op het oostelijke wad waar er nauwelijks is gevestigd en ze namen zelfs een beetje toe op de wadplaten in het zuid-zuidoosten waar niet is gevestigd en die konden profiteren van de aanleg van een beschermende dijk in 1985 en 1988.

7. Na 1988 bleven de Kanoetstrandlopers *Calidris canutus* weg van het 'noordwad' bij Griend, al nam het gebruik van het 'zuidwad' enigszins toe. Dit kon je verwachten op grond van de veranderingen in de talrijkheid van de schelpdieren die Kanoeten graag eten. Maar al met al is het huidige gebruik van het wad bij Griend door Kanoeten nog maar een fractie van wat het vroeger was.

8. In tegenstelling tot bij Griend namen op het in de luwte liggende Balgzand (waar ook minder machinaal gevestigd is) de kokkels en nonnetjes weer toe, na een inzinking in 1991 waar de visserij (in)direct verantwoordelijk voor was.

9. Onze eigen gegevens, en een uitgebreide gerefereerde literatuur, laten een nauwe samenhang zien tussen hydrodynamische en sedimentologische factoren enerzijds en recrutering en populatie-dichtheden van organismen van wadplaten anderzijds. Dit betekent onder meer dat veranderingen in schelpdier-bestanden zoals bij Griend, niet alleen te wijten zijn aan lokale sediment-verstoringen maar zelfs kunnen liggen aan (menselijke) verstoringen in andere delen van een getijdengebied.

10. De wadplaten bij Griend, maar ook andere plaatsen in de Waddenzee, lijken te veranderen van een rijke gemeenschap gedomineerd door tweekleppigen naar een biomassa-arme gemeenschap waar kort-levende kleine wormensoorten, die heel goed verstoorde sedimenten kunnen koloniseren, de dienst uit maken.

11. Over the last decade Knots in the western Dutch Wadden Sea changed their main feeding grounds quite dramatically. Not only was the northern sector near Griend abandoned after 1988, comparative data showed that birds now commute to feeding grounds much further away from their high-tide roosts than previously.

12. In the context of conclusion 10, it may be pertinent that counts at the main wintering site of several long-distance migrating shorebirds refueling in the Wadden Sea, indicate serious recent population decreases (minus 40-50% over an interval of 15 years) of predominantly mollusc-eating species such as Knots and Bar-tailed Godwits *Limosa lapponica*, and population-size increases (plus 20-40%) of polychaete-eaters such as Curlew Sandpipers *Calidris ferruginea* and Dunlins *Calidris alpina*.

13. Shellfishery-induced losses of the original bivalve stocks, and related sedimentary changes, negatively affect the many fragile elements of benthic communities and the shorebird populations dependent on it. Thus, natural processes cannot proceed undisturbed in estuarine areas (such as the Wadden Sea) where modern and large-scale shellfishery activities are permitted.

11. Gedurende de laatste tien jaar hebben Kanoeten in de westelijke Waddenzee hun foerageergebieden moeten verplaatsen naar platen die veel verder van de hoogwatervluchtplaatsen af liggen. Kanoeten moeten nu iedere getijcyclus verder vliegen en maken daardoor hogere kosten.

12. In het licht van conclusie 10 is het wellicht relevant dat tellingen in de overwinteringsgebieden van verschillende lange-afstands-trekkende steltlopers die in de Waddenzee komen bijtanken, een grote achteruitgang te zien is bij soorten die vooral schelpdieren eten zoals de Kanoet en de Rosse Grutto *Limosa lapponica* (40-50% minder na 15 jaar zonder een totaaltelling), terwijl een tweetal soorten die vooral kleine wormen eten, zoals de Krombekstrandloper *Calidris ferruginea* en de Bonte Strandloper *Calidris alpina*, in aantal zijn toegenomen (plus 20-40%).

13. De door de schelpdier-visserij veroorzaakte verliezen van de originele schelpdier-bestanden en de daardoor in gang gezette sedimentaire veranderingen, raken vooral de kwetsbare elementen van de bodemgemeenschap en sommige wadvogels. De natuurlijke processen in de Waddenzee vinden dus niet, zoals afgesproken, ongestoord doorgang zolang de huidige vormen van schelpdier-exploitatie zijn toegestaan.

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12. APPENDICES 1-5

Appendix 1. Basic numerical and biomass density data for Edible Cockles *Cerastoderma edule* in the different regions and years.

Variable	Year	Island			West			North			East			South			All flats		
		Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
Density (n/m ²)	1988	61	60	8	122	61	3	70	69	6	145	92	5	23	12	5	85	77	19
	1989	69	68	9	12	5	4	-	-	0	72	25	8	45	47	6	50	39	18
	1990	20	27	6	14	11	8	24	18	2	58	41	8	20	17	2	33	34	20
	1991	50	51	8	18	13	7	13	2	2	48	35	20	12	12	3	36	32	32
	1992	16	15	2	48	47	4	8	8	4	63	43	13	121	81	4	59	55	30
	1993	142	233	33	6	24	135	7	31	128	46	79	223	34	67	89	32	84	608
	1994	47	72	11	14	50	48	21	74	38	44	84	82	105	224	31	42	112	210
	1995	72	180	32	8	28	129	6	23	135	25	53	233	10	29	77	18	58	606
	1996	27	61	36	22	102	119	43	110	95	45	94	298	16	36	86	36	93	598
Density	1988	15	25		0	0		0	0		5	6		11	7		4	6	
Suitable	1989	51	32		6	4		-	-		24	16		30	31		22	22	
Sizes	1990	13	20		11	9		8	4		37	33		12	12		21	25	
(n/m ²)	1991	32	41		11	10		7	6		14	17		7	11		12	15	
	1992	7	6		30	38		4	5		46	45		84	69		41	47	
	1993	93	167		3	16		2	14		17	47		10	34		14	54	
	1994	24	44		4	16		17	67		17	48		69	151		22	74	
	1995	39	123		5	22		1	11		5	20		3	16		5	34	
	1996	22	54		20	97		43	110		41	91		12	30		33	91	
Biomass (gAFDM/m ²)	1988	11.71	16.02		53.76	23.12		30.44	32.45		19.55	12.49		3.06	2.12		24.05	26.01	
	1989	1.40	1.80		1.04	0.94		-	-		10.07	9.63		2.72	3.20		5.61	7.65	
	1990	2.05	2.87		2.10	1.99		5.05	4.07		6.26	5.64		2.33	1.37		4.09	4.25	
	1991	1.82	1.82		0.69	0.48		0.92	0.86		4.06	3.29		0.88	0.58		2.83	3.06	
	1992	0.41	0.31		4.18	2.95		1.20	1.08		5.27	4.52		6.92	2.19		4.26	3.08	
	1993	18.96	33.62		1.84	11.24		2.89	14.76		12.03	27.27		11.68	28.81		8.17	23.53	
	1994	1.42	2.22		0.33	20.83		0.38	1.32		2.17	5.74		2.22	4.51		2.07	10.71	
	1995	2.87	8.60		0.23	2.09		1.26	7.97		6.08	18.11		2.68	10.21		3.54	13.12	
	1996	0.39	1.98		0.25	1.39		0.19	0.54		0.58	1.81		0.56	1.90		0.45	1.61	
Biomass	1988	0.15	0.26		0.00	0.00		0.00	0.00		0.08	0.09		0.20	0.14		0.07	0.12	
Suitable	1989	0.19	0.22		0.11	0.12		-	-		0.14	0.15		0.18	0.10		0.15	0.12	
Sizes	1990	0.09	0.11		0.15	0.12		0.07	0.05		0.40	0.26		0.13	0.18		0.24	0.23	
(gAFDM/m ²)	1991	0.33	0.36		0.16	0.14		0.19	0.18		0.25	0.45		0.08	0.14		0.21	0.36	
	1992	0.01	0.00		0.35	0.49		0.08	0.11		0.58	0.58		1.36	1.06		0.55	0.67	
	1993	0.97	1.71		0.03	0.21		0.03	0.22		0.30	0.80		0.22	0.74		0.21	0.73	
	1994	0.41	0.71		0.03	0.20		0.21	0.84		0.17	0.55		0.99	2.06		0.28	0.99	
	1995	0.05	0.17		0.05	0.27		0.02	0.21		0.03	0.19		0.02	0.11		0.05	0.26	
	1996	0.06	0.15		0.17	1.08		0.19	0.54		0.37	1.24		0.07	0.31		0.26	1.03	

Appendix 2. Basic numerical and biomass density data for Baltic Tellins *Macoma balthica* in the different regions and years.

Variable	Year	Island			West			North			East			South			All flats		
		Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
Density (n/m ²)	1988	750	756	8	87	25	3	125	26	6	395	262	5	162	55	5	200	177	19
	1989	1400	839	9	230	188	4	-	-	0	650	504	8	254	267	6	423	418	18
	1990	291	357	6	59	25	8	49	2	2	179	274	8	114	55	2	111	178	20
	1991	1846	2074	8	25	18	7	66	38	2	600	637	20	565	739	3	438	592	32
	1992	187	177	2	30	18	4	30	18	4	175	103	13	94	36	4	104	95	30
	1993	303	473	33	21	36	135	35	51	128	109	156	223	78	99	89	80	165	608
	1994	171	235	11	19	30	48	31	56	38	219	442	82	178	276	31	131	313	210
	1995	83	185	32	15	31	129	25	44	135	46	63	233	30	48	77	35	67	606
	1996	277	431	36	39	67	119	130	379	95	350	468	298	315	472	86	247	424	598
Density	1988	586	528		74	21		87	23		307	145		151	56		160		121
Suitable	1989	1361	713		213	185		-	-		605	476		226	224		392		391
Sizes	1990	287	355		46	28		42	10		174	276		106	63		103		180
(n/m ²)	1991	1779	2012		18	15		63	41		573	585		557	729		418		553
	1992	184	178		34	19		29	19		167	103		90	38		99		93
	1993	238	381		18	34		32	48		85	114		69	83		65		129
	1994	154	226		18	29		29	53		177	340		151	233		109		247
	1995	73	187		12	27		23	43		39	59		26	45		30		64
	1996	271	417		35	66		126	379		339	468		307	472		240		424
Biomass (gAFDM/m ²)	1988	4.98	2.54		3.37	0.63		6.58	1.98		3.68	2.31		3.17	1.44		4.41		2.26
	1989	4.68	2.47		2.74	0.38		-	-		4.05	3.37		3.31	1.36		3.51		2.35
	1990	2.93	2.03		2.37	0.96		2.19	0.08		2.02	1.22		2.63	1.44		2.24		1.02
	1991	3.41	2.73		1.24	0.84		1.04	0.81		3.44	1.98		4.07	1.80		2.87		1.98
	1992	1.40	0.45		0.55	0.28		0.37	0.14		1.45	1.46		1.01	0.20		0.98		1.06
	1993	1.05	1.29		0.73	1.67		0.81	2.37		1.40	2.83		1.57	2.38		1.13		2.40
	1994	1.87	3.91		1.05	2.89		0.86	2.02		1.49	2.78		3.27	4.19		1.56		3.07
	1995	1.35	2.17		0.44	1.12		0.59	1.29		1.11	1.94		0.77	1.75		0.79		1.70
	1996	2.91	4.13		1.13	2.49		1.77	2.90		3.10	4.41		2.89	4.06		2.46		3.90
Biomass	1988	3.34	1.43		2.03	0.47		2.61	0.93		2.81	1.74		2.03	0.62		2.42		1.07
Suitable	1989	3.78	2.07		1.57	0.53		-	-		2.63	1.89		2.46	0.76		2.34		1.37
Sizes	1990	2.57	1.84		1.12	0.26		1.54	0.21		1.54	0.93		1.80	0.77		1.40		0.66
(gAFDM/m ²)	1991	3.02	2.40		0.46	0.28		0.74	0.39		2.74	1.47		3.37	1.78		2.18		1.64
	1992	1.22	0.38		0.52	0.24		0.34	0.02		1.03	0.90		0.84	0.19		0.76		0.66
	1993	1.04	1.28		0.45	1.04		0.48	0.91		0.96	1.47		1.30	2.13		0.80		1.43
	1994	1.15	1.72		0.67	1.41		0.66	1.53		1.10	1.89		2.08	2.88		1.07		1.94
	1995	0.97	1.74		0.32	0.83		0.48	1.15		0.77	1.39		0.57	1.28		0.58		1.25
	1996	2.14	3.56		0.62	1.59		1.34	2.30		1.91	3.36		1.90	2.42		1.56		2.83

Appendix 3. Basic numerical and biomass density data for Soft-shell Clam *Mya arenaria* in the different regions and years.

Variable	Year	Island			West			North			East			South			All flats		
		Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
Density	1988	0	0	8	0	0	3	0	0	6	0	0	5	0	0	5	0	0	19
(n/m ²)	1989	2	3	9	0	0	4	-	-	0	5	6	8	1	3	6	2	5	18
<=40	1990	1	1	6	0	0	8	0	0	2	5	7	8	1	2	2	2	4	20
	1991	51	67	8	1	2	7	7	2	2	79	199	20	22	7	3	47	154	32
	1992	1	2	2	1	2	4	0	0	4	1	3	13	12	15	4	2	6	30
	1993	4	23	33	0	0	135	0	0	128	0	0	223	1	7	89	0.5	6	608
	1994	100	212	11	4	16	48	7	25	38	123	370	82	568	1352	31	139	594	210
	1995	8	27	32	0	0	129	0	0	135	1	7	233	0	0	77	1	8	606
	1996	29	48	36	16	45	119	12	38	95	118	223	298	53	88	86	71	169	598
Density	1988	0	0		0	0		0	0		0	0		0	0		0	0	
Suitable	1989	0.5	1		0	0		-	-		3	4		1	1		1	3	
Sizes	1990	0	0		0	0		0	0		4	6		1	2		1	4	
(n/m ²)	1991	39	53		1	2		6	4		41	78		7	11		25	61	
	1992	1	2		0.5	1		0	0		1	2		10	17		2	6	
	1993	14	39		0	0		0	0		3	15		2	15		2	15	
	1994	100	212		5	18		7	25		176	506		576	1363		161	635	
	1995	8	27		1	13		2	11		10	27		11	30		7	23	
	1996	21	41		13	42		11	37		100	205		40	77		60	155	
Biomass	1988	0.00	0.00		0.00	0.00		0.00	0.00		0.00	0.00		0.00	0.00		0.00	0.00	
(gAFDM/m ²)	1989	0.05	0.12		0.00	0.00		-	-		0.02	0.03		0.00	0.00		0.01	0.02	
<=40	1990	0.11	0.16		0.00	0.00		0.00	0.00		0.02	0.03		0.06	0.10		0.01	0.04	
	1991	0.56	0.97		0.02	0.04		0.02	0.02		0.65	0.51		0.06	0.11		0.39	0.49	
	1992	0.01	0.02		0.05	0.13		0.00	0.00		0.03	0.07		0.32	0.13		0.06	0.13	
	1993	0.52	1.74		0.00	0.00		0.00	0.00		0.28	2.10		0.28	2.11		0.17	1.57	
	1994	0.66	1.59		0.12	0.45		0.10	0.39		3.96	13.91		6.16	15.34		2.54	10.69	
	1995	0.71	3.54		0.00	0.00		0.09	1.08		1.92	5.91		2.63	14.72		1.11	7.57	
	1996	0.96	2.39		0.53	2.21		0.17	0.76		3.06	8.37		1.54	3.17		1.87	6.22	
Biomass	1988	0.00	0.00		0.00	0.00		0.00	0.00		0.00	0.00		0.00	0.00		0.00	0.00	
Suitable	1989	0.00	0.00		0.00	0.00		0.00	0.00		0.01	0.03		0.00	0.00		0.01	0.02	
sizes	1990	0.00	0.00		0.00	0.00		0.00	0.00		0.02	0.03		0.00	0.00		0.00	0.02	
(gAFDM/m ²)	1991	0.28	0.91		0.02	0.04		0.02	0.02		0.31	0.26		0.06	0.11		0.19	0.24	
	1992	0.01	0.02		0.02	0.04		0.00	0.00		0.02	0.04		0.08	0.13		0.02	0.06	
	1993	0.12	0.07		0.00	0.00		0.00	0.00		0.00	0.00		0.02	0.14		0.01	0.16	
	1994	0.66	1.59		0.07	0.26		0.10	0.39		1.58	5.39		5.81	14.99		1.54	6.88	
	1995	0.08	0.32		0.00	0.00		0.00	0.00		0.03	0.24		0.00	0.00		0.02	0.22	
	1996	0.14	0.39		0.18	0.84		0.16	0.68		1.69	6.56		0.47	1.85		0.96	4.74	

Appendix 4. Basic numerical and biomass density data for Mudsnaills *Hydrobia ulvae* in the different regions and years.

Variable	Year	Island			West			North			East			South			All flats		
		Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
Density (n/m ²)	1988	12600	15100	8	1300	1800	3	-	-	6	-	-	5	12300	8100	5	9200	8650	19
	1989	33300	58900	9	500	900	4	-	-	0	4000	5000	8	11100	14200	6	5800	9500	18
	1990	4800	6200	6	0	0	8	-	-	2	2900	1900	8	20	30	2	1700	2100	20
	1991	11600	12500	8	40	50	7	300	400	2	12300	26900	20	13800	23400	3	9200	22800	32
	1992	19000	20800	2	100	200	4	50	30	4	9000	11200	13	27300	21000	4	8100	13600	30
	1993	10409	13998	33	3	23	135	375	2969	128	4103	9457	223	1012	5086	89	2298	7457	608
	1994	1512	2038	11	3	13	48	316	1535	38	2216	4464	82	2821	8041	31	1419	4341	210
	1995	840	2284	32	7	75	129	0	0	135	482	1706	233	1	6	77	231	1208	606
	1996	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Biomass (gAFDM/m ²)	1988	4.57	4.27	-	0.40	0.53	-	-	-	-	-	-	-	1.90	1.46	-	1.47	1.42	-
	1989	7.67	10.60	-	0.03	0.03	-	-	-	-	3.53	4.42	-	2.37	3.13	-	2.36	3.53	-
	1990	1.32	1.84	-	0.00	0.00	-	-	-	-	2.76	1.94	-	0.03	0.04	-	1.58	2.01	-
	1991	3.57	3.51	-	0.00	0.00	-	0.03	0.05	-	3.34	4.58	-	1.60	2.76	-	2.28	3.97	-
	1992	4.14	4.39	-	0.05	0.09	-	0.01	0.01	-	4.08	4.58	-	3.05	2.06	-	2.34	3.67	-
	1993	3.08	4.23	-	0.00	0.01	-	0.12	0.91	-	1.26	2.90	-	0.31	1.56	-	0.70	2.27	-
	1994	1.62	2.36	-	0.00	0.01	-	0.34	1.59	-	2.51	3.83	-	1.52	3.02	-	1.35	2.97	-
	1995	1.96	5.32	-	0.02	0.17	-	0.00	0.00	-	1.48	4.61	-	0.00	0.03	-	1.03	3.87	-
	1996	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 5. Basic numerical and biomass density data for the polychaete worms *Nereis diversicolor*, *Nephtys hombergi* and the Capitellidae family, and for the isopod crustacean *Urothoe poseidonis*.

Variable	Year	Island			West			North			East			South			All flats		
		Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
Density (n/m ²)	1993	43	70	33	9	32	135	4	17	128	23	48	223	47	85	89	19	50	575
	1994	106	93	11	112	149	48	56	90	38	201	167	82	233	248	31	157	178	199
	1995	109	96	32	39	96	129	23	58	135	96	99	234	138	154	77	72	108	575
	1996	166	197	36	69	89	119	70	98	95	238	289	294	244	286	86	178	250	594
Density (n/m ²)	1993	0	0	27	14	33	135	21	35	130	12	26	223	18	32	89	14	30	610
	1994	0	0	11	3	13	48	24	79	38	2	10	82	0	0	31	6	36	210
	1995	2	13	26	8	25	129	12	35	135	11	41	233	7	23	77	10	33	606
	1996	5	17	27	29	46	119	27	54	95	12	36	297	5	20	86	16	40	633
Density (n/m ²)	1995	139	217	32	24	261	129	142	243	135	138	217	234	117	155	77	156	229	575
	1996	111	202	36	75	141	119	78	127	95	182	275	298	85	141	86	131	223	598
<i>Capitellidae</i>																			
Density (n/m ²)	1995	156	135	32	84	135	129	75	145	135	316	319	234	166	207	77	156	187	261
	1996	109	139	36	244	242	119	347	305	95	183	245	298	241	289	86	131	230	267
<i>Scotoplanes</i>																			
Density (n/m ²)	1995	45	137	32	228	545	129	539	899	135	153	358	234	84	256	77	251	586	575
	1996	0	0	36	27	62	119	110	282	95	17	78	298	2	14	86	32	132	598
<i>Urothoe</i>																			

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